Examining the effects of *in-situ* aquaculture on marine ecosystem structure and function

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Abstract

Marine aquaculture operations in Atlantic Canada have been steadily increasing for decades. Along Newfoundland's southern coast, Atlantic salmon (*Salmo salar*) are farmed in two of the three major oceanographic bays, and development of hatchery and farm operations in the third are ongoing. Marine farm operations attract wild animals, and resulting changes to local ecosystem properties may also affect wild salmon during coastal phases of their marine migrations to and from their natal rivers. In this thesis, I explore the mechanisms responsible for the aggregative effect generated by farm activity, and examine the effects of changing ecosystem properties on wild salmon populations with natal rivers in close proximity to farm operations. I show that fish schools are an effective proxy measure for predation risk, and that in sea cage environments, attraction of large predators to active farm sites can be quantified using acoustic measurements of fish schools. I also show that basal resource availability does not differ between active and fallow farm sites, while basal productivity trends differ annually between bays and as well across years within the same major oceanographic bay regardless of the presence of aquaculture operations. Finally, I show that wild salmon exhibit little fidelity to active farm sites compared to farm fish, and differences in movement behavior and changes to local ecosystem properties resulting from farm activity leads to increased mortality risk via natural predation for escaped farm-raised salmon. Cumulatively, results from this thesis suggest that marine pelagic ecosystems and natural processes therein are changing in response to aquaculture activities. Within these changing ecosystems, marine survival for escaped farm salmon is likely low due to the combination of reduced antipredator behavior and fidelity to active farm sites where encounter probability with naturally-occurring predators is high.

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Co-authorship Statement

All work contained within this thesis was performed by Michael Piersiak, with the guidance and supervision of Dr. Mark Abrahams. This thesis is presented in manuscript format, with four data chapters lying intermediate to a general introduction and general conclusion. For all data chapters, experimental design, field data collection, data analysis, manuscript writing, and preparation of figures and tables was done by Michael Piersiak and Dr. Abrahams.

Chapter 1. General Introduction and Overview

Ecosystems are structured by a combination of biotic and abiotic factors. Mainly, all organisms and physical features of an environment make up the structure of a given ecosystem. Subsequently, interactions between organisms, and between organisms and the physical environment that result in the production and flow of energy through the ecosystem, constitute how the respective ecosystem functions (Myster 2001). In more simplified terms, the way ecosystems function is the result of bottom-up and top-down forces, and how these two force sets interact to shape the flow of energy through the system. Bottom-up forces are created by primary productivity and the upward flow of energy through food webs, and are affected heavily by the abiotic environment. Conversely, top-down forces are the result of predators that regulate prey demographics through direct (consumptive) and indirect (non-consumptive) mechanisms (see Lima 1990 and Gaynor et al. 2019; Peckarsky et al. 2008 for examples), where consumptive effects are the result of direct removal of animals from a population and non-consumptive effects are fear driven effects that cause animals to alter behavior in response to mortality risk, and can have the most significant impact on ecosystem structure and function (Leroux and Schmitz 2015).

Particularly with respect to predation risk, the manifestations of top-down and bottom-up forces on ecosystem structure and the behavior of animals within have been studied extensively in terrestrial and aquatic systems (e.g. Rip & McCann 2011), while pelagic marine systems (deep water and largely lacking physical structures present in other marine habitats that may provide immediate physical refuges from predators) have received comparatively less attention despite constituting a large proportion of the world's oceans. Significant focus in terrestrial systems has been devoted to consumer-resource relationships, and how enriching ecosystems with limiting resources can destroy that ecosystem's steady state through the 'paradox of enrichment'

(Rosenzweig 1971). Marine pelagic ecosystems have been traditionally thought of as bottom-up limited, but are also heavily affected by top-down forces that cascade through the entire food web (Verity & Smetacek 1996), and our mechanistic understanding of both force sets in pelagic ecosystems is limited predominantly to studies assessing changes in population levels of pelagic species over time from fisheries and catch data (Baum & Worm 2009). Although this informs on population-level consequences of consumptive effects (how direct removal of individuals influence population structure), it fails to encapsulate non-consumptive top-down effects (the 'landscape of fear;' see Gaynor et al. 2019), which may influence the spatial outcome of predator-prey interactions (Hammond et al. 2012).

Recent application of acoustic survey techniques has revealed periods of dynamic food web activity directly affected by both bottom-up and top-down processes in marine pelagic systems (Benoit-Bird & McManus 2014). However, we are still lacking a methodology for quantifying predation risk in pelagic marine environments that does not rely on direct measurements of predators/predation risk which are often difficult to obtain as marine top predators are often highly mobile and can travel extensive distances (e.g. Richardson et al. 2016). These ecosystems also typically lack physical structures present in other marine ecosystems that provide immediate refuge from predators (e.g. coral reefs) which limits behavioral options available for animals to both find food and maximize foraging efficiency while remaining relatively safe from predators. Many pelagic fish species rely on schooling behavior to increase foraging efficacy (Pitcher 1986) and control predation risk (e.g. Ioannou et al. 2011), yet the dynamics of schooling behavior are often described as a byproduct of a predetermined stimulus (e.g. behavioral responses of fish schools to direct predation risk; Nøttestad et al. 2002) rather than as cumulative sum of various environmental processes/factors. While these data have

provided a strong understanding of the dynamics of group behavior in response to specific factors (see Krause and Ruxton 2002; Rieucau et al. 2015), quantifying and describing behavioral patterns over larger scales in pelagic ecosystems is often difficult as accurate descriptions of behavior require knowledge of ecosystem processes that directly affect the respective animal and associated behavior of interest. Difficulties associated with direct measurements of large-bodied pelagic predators has led to a lack of study from these ecosystems, and in chapter two of this thesis, I test the effects of predation risk of groups of fish in a laboratory experiment, and apply knowledge gained from these results to interpret patterns in fish school dynamics present over large spatial scales from hydroacoustic field data. Marrying these two data streams will provide a means of quantifying risk effects generated by large, piscivorous predators on fish schools without directly measuring the relative abundance and distribution of these predators themselves. In this chapter, predation risk refers to the effects exerted by piscivorous predators on schooling fishes, and these data will provide a method for assessing the relative impacts that human activities have on large pelagic predators, and also provide a potential means of quantifying the relative abundance of predators across large spatial landscapes. Human activities have significant effects on natural processes with large bearing on ecosystem structure (Madin et al. 2016), and determining their effects on large predators, which also have significant bearing on ecosystem structure, can help map ecosystem effects of marine anthropogenic activities.

Human activities have clear effects on the behavior of marine species as well as the structure of the ecosystems they occupy. For example, removal of marine top predators via overfishing has led to the trophic downgrading of marine food webs (Estes et al. 2011). As well, human infrastructure in the ocean has a strong aggregative effect on marine species (e.g.

Dempster et al. 2009; Trygonis et al. 2016; Moreno et al. 2016), which can affect larger ecosystem structure by altering distributions of marine organisms at large spatial scales (e.g. Uglem et al. 2014). Pelagic ecosystems, however, are so large that obtaining data at scales relevant to the question of interest can be logistically challenging due to the extensive ranges of some pelagic species. However, spatiotemporally predictable aggregations of wild marine organisms that result from various human activities provide unique opportunity to study the dynamics of pelagic ecosystems, as such aggregations only occur over very brief temporal windows in undisturbed environments (Benoit-Bird & McManus 2014). Few studies have measured direct behavioral interactions between pelagic animals, and as well between animals and their environment, and been able to associate these interactions with food- and fear-driven effects (top-down and bottom-up processes) (see also Benoit-Bird & Au 2003). The ability to study these instances are rare in part due to the logistical difficulties as larger pelagic predators are often highly mobile and consequently difficult to study, but persistent fish aggregations around sea farms (Dempster et al. 2004) may afford the ability to observe these interactions due to the attraction of predators to these sites (Uglem et al. 2014), and identify factors allowing these aggregations to persist over significantly longer time intervals than observed in a natural setting (see Benoit-Bird & McManus 2014).

On the south coast of Newfoundland, marine salmon farm operations affect the distribution of marine organisms at large spatial scales (Goodbrand et al. 2013), yet the mechanisms that underlie the persistence of these aggregations are still unclear. Since Goodbrand et al. (2013) surveyed Fortune Bay in 2011, all sites previously licensed have contained active salmon farms, and productivity cycles at these sites interspersed with fallow periods that serve to prevent waste buildup and maintain infrastructure integrity (perform routine

maintenance on net-pens to minimize probability of fish escapes). These sites provide food and physical structure that is atypical of pelagic environments due to the predictability of both resources, and in this thesis, I therefore examine the effects that aquaculture activities have on top-down and bottom-up processes, as food and predators are major determinants of ecosystem structure and function. I address this by examining the distribution of fish (e.g. herring (*Clupea harengus*) and mackerel (*Scomber scombrus*)) with respect to both primary productivity levels and relative distribution of schooling, planktivorous fish predators such as blue sharks (*Prionace glauca*) and tuna sp. in pelagic environments containing sea farm sites with recent history of active fish farming.

Along with ecosystem-level effects, concerns exist regarding interactions between wild salmon populations and marine aquaculture operations in areas of high farming intensity (Keyser et al. 2018). In Newfoundland, the aquaculture industry has been increasing in scale since the late 1990's. Production of salmonids in Newfoundland nearly quadrupled from 2014-2015 (5,980—19,684 metric ton increase; Statistics Canada 2014; Statistics Canada 2015), and increased 29.1% between 2015 and 2016, rising from 19,698 to 25,411 tonnes (Statistics Canada 2016). Along the Coast of Bays substantial industry presence already exists in two of the major oceanographic regions (Bay d'Espoir and Fortune Bay), and plans for expansion in to the last of the major regions (Placentia Bay) have been recently approved. Comparatively, New Brunswick, Canada, has been producing Atlantic salmon since the late 1970's, and saw major industry expansions in the mid-1980's and again from 1994-2000 (Chang et al. 2014). However, industry expansion has since been limited by outbreaks of infectious salmon anemia (ISA), and production statistics leveled out in the wake of major ISA outbreaks in the early 2000's (Chang et al. 2014). Consequently, the study of aquaculture-environment interactions in this area has

focused on ISA (Chang et al. 2007; Chang et al. 2014); and as well on the effects of organic enrichment on benthic communities which have shown significant impacts of farm waste on nutrient fluxes through coastal ecosystems (Strain & Hargrave 2005). In the eastern Atlantic Norway and Scotland have been producing salmon since the 1960's (Thorstad et al. 2008) and have subsequently had more time to gather information regarding the environmental impacts of aquaculture activities, particularly with respect to impacts on and threats to wild salmon populations whose natal rivers coincide with areas containing significant salmon farming activities. Data from this region has shown significant spread and genetic introgression in the majority of salmon rivers across Norway (Karlsson et al. 2016), which poses significant risk to the health and viability of wild populations (Bolstad et al. 2017). Genetic introgression has received substantial focus due to the importance of localized genetic adaptations in wild populations and the potential for dilution via hybridization with farm fish (Wringe et al. 2018; Sylvester et al. 2019; Taranger et al. 2015; Fleming et al. 2000), and effects such as resource competition and disease/parasite transfer have also seen significant attention (Naylor et al. 2005; Madhun et al. 2017). However, Atlantic salmon are an anadromous species, and data describing the marine behavior of farm escapees and resultant interactions with wild salmon populations in the ocean are limited (but see Hamoutene et al. 2018; Skilbrei et al. 2014) compared to the body of knowledge describing interactions in freshwater environments. Farm salmon are known to escape marine net pens throughout the species' native range (Skilbrei et al. 2014; Keyser et al. 2018), and initial exposure to wild populations often occurs in the ocean. Describing interactions in the marine theatre will therefore help to understand factors that determine relative risk to wild populations in the ocean prior to freshwater spawning migrations.

Wild salmon spend a significant portion of their life cycle in marine environments. Factors affecting the worldwide decline of wild salmon populations have been attributed in part to the collapse of pelagic food webs in the North Atlantic and the subsequent effects on the feeding ecology of salmon (Jonsson et al. 2016), but aquaculture-related environmental changes may also contribute to declines in salmon populations during critical marine phases where salmon migrate to and from their spawning grounds amongst areas of high farm intensity. In Canada, wild salmon populations in regions with high farm activity have been declining for decades (DFO 2017). A recent study has shown that farming intensity (# farms per unit area) can be used as a barometer for escape and introgression risk (Keyser et al. 2018), but our understanding of the mechanisms underlying this phenomenon is limited. Farm salmon escape containment at all life stages (Skilbrei et al. 2015), and Madhun et al. (2017) found that the majority of farm fish entering rivers were infected with one or more farm-associated diseases. Although significant interactions between farm and wild populations have been documented in fresh water, farm fish typically escape containment in the ocean and the first interactions with wild populations likely occur during marine phases of their life cycles. Farm fish have shown reduced responses to predation risk (Biro et al. 2004) and have also exhibited site fidelity to farms in freshwater environments (Charles et al. 2017) despite rapid dispersal after initial escape event (Hamoutene et al. 2018; Skilbrei 2015), which likely differ from the behavior of wild populations that have adapted to local environmental conditions. Such behavioral differences likely have consequences for survival rates of the two populations in the ocean, and in the fourth chapter of this thesis, we describe the movement of groups of farm and wild salmon in environments containing high farming intensity as these data will provide information on habitat

use and subsequent potential sources of mortality for both populations that result from aquaculture-related changes to pelagic ecosystems.

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Chapter 2. The morphological parameters of fish schools are an effective proxy measure for predation risk at large spatial scales

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Abstract

Predation risk and its various subcomponents have significant effects on ecosystem structure and the behavior of animals therein. In pelagic marine environments, logistical constraints have limited our ability to quantify predation risk and its effects on ecosystem structure, and reliance on concurrent, quantitative measures of both predators and prey to do so is often logistically challenging. However, pelagic fish rely heavily on schooling behavior to manage predation risk, and the growing number of studies that have directly quantified the dynamics of school behavior in response to different marine predators have provided a strong understanding of group behaviors resulting from different levels of predation risk, and subsequently a behavioral metric by which predation risk can be assessed without making direct observations of predators themselves. In our study, we used the index of dispersion to determine if changes in school behavior resulting from variation in predation risk levels could be detected in a tank-based experiment. We then used hydroacoustic survey data to determine if patterns in school morphology observed in the field could be used as proxy measures for predation risk across the larger spatial environment. Groups of fish in the lab showed significant responses to simulated encounters with predators, but no behavioral responses were observed in response to perceived predation risk. Similarly, our hydroacoustic data showed no differences in school sizes between areas of high and low endemic risk levels, but schools found in areas with high predator abundance were significantly more vertically stratified, suggestive of an increased ability to detect predators. Overall, these results suggest that the effects of direct predation risk on fish school behavior can be directly quantified without data describing predator distributions, and patterns in school dynamics can be used to characterize relative risk of encountering predators across large spatial environments.

Introduction

The influence of predators on the structure of marine ecosystems is well known (Burkholder *et al.* 2013; Estes et al. 2011; Myers et al. 2007; Frank et al. 2005; Lima & Bednekoff 1999; Lima & Dill 1990). However, our understanding of the mechanisms through which predators exert this influence, are not. Predators affect ecosystems directly by consuming prey items and subsequently regulating the abundance of prey populations via consumptive effects, and also indirectly (non-consumptive effects) through the 'landscape of fear' where perceived risk determines the spatial distribution and level of antipredator behavior exhibited by prey (Gaynor et al. 2019). Combined, direct and indirect (consumptive and non-consumptive) effects of predators constitute the cumulative effect of predation risk. Non-consumptive effects influence animal behavior over varied scales (Brown et al. 1999; Schmitz et al. 2004; Hammond et al. 2012), and can induce behavioral effects orders of magnitude greater than direct and potentially lethal interactions between predator and prey (Ripple & Beschta 2004; Madin et al. 2016; Hasenjager & Dugatkin 2017). These effects have been extensively studied, providing an understanding of the ecological signals and patterns in prey behavior in a wide range of ecosystems (Lima & Dill 1990 for examples), yet pelagic marine environments present significant logistical constraints to studying predator-prey interactions, which has challenged our ability to quantify predation risk and its effects on pelagic ecosystem structure and function.

Strategies employed by prey to reduce their risk of predation include changes in the foods they consume, social structure, and when and where they are active (Clark & Levy 1988; Werner et al. 1984). However, animals must locate and consume food to meet basic energetic needs, and the combined influence of predation risk and foraging needs shapes ecosystem-wide patterns in animal distributions across large and small scales as animals search for food while attempting to

avoid being consumed by a predator. Access to data with high spatial and temporal resolution from pelagic marine environments has shown higher degrees of spatial co-occurrence between predator and prey than previously documented (Benoit-Bird & Au 2003; Wirsing et al. 2007), and suggest that the ability to quantify the dynamic spatial distribution of predators and prey over variable spatial and temporal scales in these environments may provide new insights into marine predator-prey relationships (Russell 1992).

Pelagic environments lack physical structures that provide immediate physical refuge from predators, limiting behavioral options that help animals control predation risk and maximize foraging efficacy. Patchily distributed resources (e.g., food, structure, etc.) characteristic of most marine environments (Steele 1978) have significant effects on animal behavior, and physical structure especially can facilitate high degrees of spatial co-occurrence between predator and prey without subsequent increases in prey mortality rates (Wirsing et al. 2007; Lima 1992). For pelagic fish without access to physical structure, aggregation is a form of hiding in plain sight, and helps to manage predation risk across variable spatial scales (Ioannou et al. 2011; Turner & Pitcher 1986). However, aggregation comes at a cost. Increases in group size increase intraspecific competition for food resources, and if group size becomes too large, the costs of group membership may outweigh the benefits.

The costs and benefits of group living are well known (Krause & Ruxon 2002), and in the most basic sense, the size of a given group is determined by the amount of food available for individuals relative to the risk of predation associated with living in that group. While there are benefits associated with larger group sizes (e.g. risk dilution (Foster & Treherne 1981), predator confusion, encounter dilution), competition for different resources ultimately limits group size. For pelagic fish that rely on schooling behavior to control predation risk (Ioannou et al. 2011;

Nøttestad & Axelsen 1999; Nøttestad et al. 2002; Pitcher et al. 1996; Nottestad et al. 1996) and find food (Pitcher et al. 1986), school size and morphology is a reflection of food availability and predation risk levels as perceived by individuals within the school. Although optimality reasoning has typically been used as a tool to identify group sizes that maximize the fitness of individuals within the group given a set of environmental variables (reviewed in Pulliam & Caracao 1984; Lima & Dill 1990), the dynamic relationship between animals and their environment causes the size and behavior of a given group to fluctuate in response to variation in energetic states (Alonso 2002; McNamara & Houston 1990) and changing environmental conditions (Williams et al. 2013). In Norway, schools of spring-spawning herring varied in size by up to four orders of magnitude depending on the motivational state (feeding, spawning, searching, immigrating, and emigrating) of individuals within the group (Nøttestad et al. 1996). In pelagic habitats where predation risk (Magurran 1990) and foraging benefits (Pitcher 1986) are often cited as the primary drivers of school formation and maintenance, quantitative measures of group dynamics may be a useful means of developing our understanding of the effects of risk on ecosystem structure.

Despite significant study in a diverse range of habitats (Lima & Dill 1990), the dynamics of group behavior remain significantly understudied in marine pelagic ecosystems. The growing number of studies performed in these environments have provided us with a basic understanding of pelagic predator-prey systems (Wirsing et al 2007; Benoit-Bird & Au 2003; Nøttestad et al. 2002; Nøttestad & Axelsen 1999; Nøttestad et al. 1996), and the associated role that aggregative behaviors play in controlling predation risk outside of direct and potentially lethal encounters with predators (Ioannou et al. 2011). These studies have shown that rapid and synchronized alterations to school morphology are effective antipredator behaviors (Nøttestad et al. 2002; Axelsen et al. 2001; Nøttestad & Axelsen 1999; Nøttestad et al. 1996), and predictions from laboratory

environments also suggest that increasing vertical stratification may provide antipredator benefits to groups of fish (Abrahams & Colgan 1985). The main benefit of vertical stratification in fish schools is increasing the number of individuals that are visually able to detect an approaching predator. This requires close clustering (increases in school density or packing) of individuals to confer visual detection capabilities on the highest number school members, while maintaining the ability to effectively outmaneuver a predator by rapidly altering school morphology. Vertical stratification are therefore relative to school packing density, as schools can have similar vertical profiles within the water column, but have different horizontal profiles which affect overall packing density of the entire school, as well as the visual detection capabilities. However, behavioral responses to predation risk are also scale dependent (Hammond et al. 2012; Hunsicker et al. 2011; Levin 1992), and prey responses to direct encounters with predators likely differ significantly from prey behaviors caused by the fear of predation risk (e.g. Schmitz et al. 2008). Various techniques have been used to measure aggregative behaviors (Hunter 1966; Cullen et al. 1965; Keenleyside 1955; Breder 1954), yet access to field data simultaneously quantifying risk effects across larger environments has been limited, and with the exception of few studies (Benoit-Bird & McManus 2014; Benoit-Bird & Au 2003), attempts to directly quantify the effects predation risk on the spatial structure of animal groups throughout an environment have been limited.

Recent studies from pelagic marine environments have utilized different acoustic methodologies to describe and quantify the behavior of individual fish schools (Gerlotto et al. 2010; Gerlotto & Paramo 2003), as well as examine aggregative patterns of fish schools in response to different environmental factors (Jech et al. 2012; Nakamura & Hamano 2009). The high spatial and temporal resolution provided by acoustic data has allowed scientists to observe

behavioral patterns resulting from both individual fish schools encountering predators, as well as behavioral patterns of predators and prey responding to ecological processes that operate over larger spatiotemporal scales (Certain et al. 2011; Benoit-Bird & Au 2003). Despite this, however, the use of hydroacoustics in marine pelagic ecosystems has largely focused on the behavior of individual schools of fish, while few studies have examined how predation risk influences the behavior of groups across broad spatial scales. As such, our goal was to first determine if we could detect changes in aggregative behaviors of fish in a laboratory setting, and secondly to use these data in combination with our knowledge of behavioral signals indicative of predation risk generated by fish schools with acoustic methodologies to test whether the aggregative behaviors of fish schools can be used as indicators of predation risk in marine pelagic environments, as this will provide an avenue for researchers to examine the effects of predation risk on ecosystem structure, without significant investment in quantitative measures of predators themselves. We expect that groups of fish in high-risk environments will display much more risk averse behavior in the form of increased packing density, while the behavior of fish in low-risk environments will comparatively less indicative of risk-effects where fish will be less densely packed.

Methods

We measured the impact of predation risk on fish schools in lab and field environments. In the lab we created a controlled environment, and used a two-factor design to directly measure changes in aggregation levels of fish in response to the effects of environmental (an animal's perception of risk levels independent of direct encounters with a predator) and direct predation risk. In the field, we used hydroacoustic methods to determine if we could detect similar responses to predation risk by examining changes in the aggregative patterns of fish schools, and

use these behavioral differences as indicators of the level of risk endemic to the environments these schools occupy.

Laboratory Experiment:

Marine three-spined sticklebacks (*Gasterosteus aculeatus*) were chosen as our experimental species due to their high local abundance, hardiness in laboratory environments, and presence of alarm pheromone in their skin (Brown & Godin 1997). Sticklebacks were captured locally (approx. 40km from lab) in May 2014 from Indian Pond, Seal Cove, NL (47˚27'19.42"N, 53˚05'31.98"W) using a beach seine by the Department of Ocean Sciences' Field Services Unit. After capture, fish were immediately transported to the lab in 88l oxygenated coolers, and transferred to 500L holding tanks. Fish were fed *ad libitum* daily with crushed pellet feed while in holding tanks, and maintained at ambient temperature (4.4-11.3˚C) and light cycle for the duration of the experimental period. All fish used during experimental trials were young of the year, as many captured adults were gravid females or males in spawning colors and territorial spawning behaviors of males may have had adverse effects on schooling behaviors. Six-hundred young of the year fish were retained from the initial group of captured fish and used for experimental trials (mean ± SD: 33.04±5.4 mm), while adults in breeding condition were kept in a separate holding tank and used only for alarm pheromone extraction.

Alarm pheromone was used to simulate direct encounters with a predator, and was extracted using the procedure described by Brown & Godin (1997). Five sticklebacks were sacrificed per trial first by Eugenol overdose (60mg/l, see Keene et al. 1998) followed by a subsequent blow to the head (as recommended by Canadian Council on Animal Care guidelines). Skin fillets were removed from both sides of each fish using a scalpel and forceps, and

homogenized with 50 mL chilled, distilled water (herein 'DI water') using a mortar/pestle. The solution was then run through filter paper to remove any suspended particulates, and all alarm pheromone was kept on ice and made fresh immediately prior to use. All instruments were cleaned with ethanol between pheromone extraction on individual fish.

Experiments were conducted in a 4.8m diameter, round flow-through (30L/min) tank (**Figure 2.1**), filled to a depth of 30cm with ambient (4.4-11.3˚C) surface seawater and covered with a black, opaque tarp to avoid external disturbances. Fish were exposed to ambient light (100 lux)/dark cycles. Within the tank there were two downward-facing Axis 221 day/night network cameras (Axis Communications: Lund, Sweden) connected to the laboratory network to provide live recording capabilities at 45 fps (640x480 pixels). The field of view for each camera covered one-half of the experimental tank, and prior to all trials, camera settings were checked to ensure no differences in focus or field of view between the two. Two cameras were used because the tank covering did not allow us to mount a single camera high enough to observe the entire tank. After trials were completed, images from the two cameras were merged along the center line of the tank to ensure that multiple observations of the same fish did not occur. Tygon tubing extended from the exterior to the middle of the tank along the underside of the tank cover (total volume of 50mL) to remotely inject distilled water or an alarm pheromone as an experimental stimulus while not providing any visual cues to the fish.

To examine the effects of predation risk on the aggregative behaviors of fish, we created controlled environments with either high or low environmental risk levels, and measured behavioral responses of stickleback groups to simulated direct encounters with a predator. Environmental risk was simulated by altering hunger levels of experimental fish (Hartman & Abrahams 2000), as hungry animals view the world as safer than well fed animals. Direct

encounters with predators were simulated using the alarm pheromone. Food treatments used to simulate environmental risk levels were implemented for 48 hours prior to all trials, where fish were starved for the 48hr duration or fed daily to satiation (uneaten food was flushed from tanks post-feeding) to simulate low and high environmental risk levels respectively. This led to a 48-hr gap between each trial, during which fish in the experimental tank were fed ad-libitum or starved depending on the experimental treatment, and fish in the holding tank were always fed once daily. In total, this experiment consisted of four different combinations of environmental risk and experimental stimuli. Individual trials were conducted at each environmental risk level, and fish were exposed to either alarm pheromone to simulate direct encounters with predators, or distilled water to control for the effects of the alarm pheromone.

For each trial, 100 sticklebacks were randomly selected without replacement from a holding tank containing 600 fish and placed in the experimental tank 48 hours prior to trials in order to acclimate to the tank. After the trial, fish were placed in a new holding tank, until 6 trials were completed and all fish from the initial holding tank had been used. Groups of 100 were then randomly selected again from the new holding tank and this procedure repeated until 18 trials were complete, and each fish was used for 3 total trials constituting 18 independent experimental observations (see **Table 2.1** for order). Had we kept schools together and schools were to follow bold individuals, behavioral measurements would then be reflective of only a small subset of individuals, where by mixing schools instead, we effectively randomized grouped individuals across trials. We chose groups of 100 because it was a substantial enough group size to observe schooling behaviors. We were also constrained by our tank and analysis capabilities. To many fish would have prevent effective counting of individuals, and 100 fish allowed us to effectively account for all individuals while schooled.

The behavioral response of the stickleback to the environmental conditions was obtained in 20 minute, video-recorded trials based on results from Brown and Godin (1997) who used 8-minute intervals between pre- and post-stimulus injection periods (16 total minutes) to observe the effects of alarm pheromone on sticklebacks. The 50mL batch of experimental stimulus was introduced to the tank at the tenth minute from a syringe attached to the tygon tubing. The tubing was immediately flushed using 50mL chilled distilled water to make sure the entire batch of stimulus entered the tank, similar to the procedure performed in Brown & Godin (1997). One image was then taken from video recordings at each 1-minute interval (starting with time=0), leaving each trial with 22 total images (11 before stimulus introduction, 11 after). We used ImageJ (Schneider et al. 2012) image analysis software to divide each tank image into 241 quadrats (each $0.0625m^2$) and recorded the number of fish in each quadrat. We quantified the spatial response of the sticklebacks to the stimulus by calculating the index of dispersion (Krebs 1989), or the mean to variance ratio associated with the number of fish present in each quadrat where:

$$\textit{Index of Dispersion (I)} = \frac{\text{Observed Mean}}{\text{Observed Variance}} = \frac{\bar{x}}{s^2}$$

Increases in the index of dispersion indicate a greater level of aggregation.

During our experimental period, we only ran three trials consisting of low environmental risk X distilled (DI) water and three trials consisting of high environmental risk X DI water. We limited these treatments to three trials each due to low variance in aggregation indices. For the remaining two combinations of environmental and simulated direct predation, we observed much

larger variance between individual trials, and therefore added additional replicates to these risk treatments for a total of six trials each.

Analysis

For each experimental trial, index of dispersion (I) values were calculated pre- and post-stimulus introduction from images taken at each one-minute interval (n=11 before stimulus, n=11 after stimulus). We tested for differences in values of I between pre- and post-stimulus treatments. We averaged index values from pre- and post-stimulus treatments for each trial, and compared the difference in these values [$\text{mean}(I)_{\text{after}} - \text{mean}(I)_{\text{before}}$] across risk treatments. We used the index of dispersion to test for changes in aggregation levels caused by the combined effects of hunger level (HL) and stimulus treatment (pheromone/DI water; abbreviated to 'ST') using a two-way ANOVA, where:

$$\Delta I \sim HL + ST + HL*ST$$

Hydroacoustic Surveys:

Four hydroacoustic surveys were performed between September 2014 and September 2016 at Atlantic salmon (*Salmo* salar) aquaculture sites on the south coast of Newfoundland from Harbour Breton (47°28'23" N, 55°50'06" W) through Fortune Bay (47°35'49" N, 55°24'32" W) (**Table 2.2**). A total of 14 different bays containing active or fallow Atlantic salmon aquaculture sites were surveyed (**Figures 2.3 & 2.4)**. Active sites contained between 8 and 24 circular net-pens, each 10m diameter and approximately 20m deep. Active cages contained salmon ranging from post-smolt to adult, and different age classes were segregated between bays. Our surveys took place over a three year period, and 9 of 14 bays were surveyed during active and fallow

periods (between surveys) due to the timing of fish stocking/harvesting. Fallow sites were those containing no active salmon aquaculture at the time of surveying, but still with barebones farm infrastructure such as cages without netting, and/or perimeter marker buoys. We considered active farm sites as 'high risk' locations, as farm activity has been shown to attract significant amounts of wild fish compared to similar locations with no aquaculture (e.g. Dempster et a. 2009), and as well large fish attracted represent a significant predation threat to fish aggregations around farms (Serra-Llinares et al. 2013).

Hydroacoustic surveys were conducted aboard a 10m dedicated hydroacoustic research vessel the RV Gecho II. Data were obtained using a Simrad EK60 38/120kHz split-beam transducer **(Table 2.3).** Our echosounder was calibrated prior to each survey using a standard tungsten-carbide sphere (see Simmonds & Maclennan 2008). Transducers were mounted off the port beam on a winch system, allowing for easy deployment and retrieval. Data were recorded directly on ship-board computer systems that also provided live viewing capabilities.

We used a randomized transect method to survey each bay, and sampling effort devoted to each bay was based on bay area relative to total area sampled (**Table 2.4**). Goodbrand et al. (2013) showed that the aggregative effect of sea farms on fish in this location occurred at the bay level, rather than just the immediate vicinity of the net pens, and we were therefore able to allocate our survey efforts to the entire bay rather than only the immediate vicinity of the net pens. Transects were run parallel to the bay entrance at 5-7kt, and encompassed the entire spatial range and depth profiles of each bay. Transect locations within each bay were randomly selected from the total number of non-overlapping transects possible within each bay (as a function of bay area and acoustic beam width). For smaller bays, the minimum number of transects performed was 3.

Analysis:

Echoview software (version 7.0.97) with the schools detection module (**Table 2.5**) was used to analyze our data. Biomass estimates of individual schools are displayed as nautical area scattering coefficients (NASC; MacLennan et al. 2002), and were obtained via the horizontal average of vertically integrated of echo signals in the water column across 1.0 nautical mile sampling units. The schools detection module also provided estimates of school morphological parameters which allowed us to test for differences between high- and low-risk areas. Estimates of vertical stratification were obtained by dividing the maximum observed horizontal dimension (length) by the maximum observed vertical dimension (height) of schools. We chose to examine school size and vertical stratification as indicators of predation risk because larger group sizes dilute risk experienced by individuals within the school by reducing attack probability (Foster & Treherne 1981), and schools of fish sacrifice hydrodynamically efficient discoid structures in favor of compact, vertically stratified structures when predators are present (Abrahams & Colgan 1985). We tested for differences in both biomass and vertical stratification between control (fallow) and treatment (active) bays using a t-test.

Results

Laboratory Experiment

Prior to each trial in our experiment, the tank inflow was shut off to allow fish to acclimate prior to the start of the trial, as well as to make fish visible on our cameras. During this 30-minute period prior to trial start, fish were observed in loose aggregations, and were rarely observed moving around the tank. During our 48-hr acclimation period to the experimental tank when the water

inflow was active, groups of sticklebacks were slightly more mobile than pre-experimental periods. However, turning off the water flow appeared to have no effect on the formation/maintenance of groups as it caused only a slight reduction in the mobility of fish in the tank that was likely due to the tank current created by the inflow.

Our experimental trials took place from Aug-Oct 2015, and in all experimental trials (n=18) tank water conditions were maintained at ambient sea-surface temperature (SST). During the 3-month period of our study, temperature ranged from 11.3°C to 4.4°C, and comparing values of I from pre- and post-stimulus periods allowed us to analyze our data independent of potential temperature effects, and we found that the alarm pheromone had the strongest effect on aggregative behavior ($F_{1,14}$ = 4.27, p = 0.057), while environmental risk ($F_{1,14}$ = 0.43, p = 0.52) and the interaction between hunger level and stimulus treatment ($F_{1,14}$ = 0.225, p = 0.64) showed no significant effect (**Figure 2.4**). In trials using DI water, mean index value for pre-stimulus injection was 1.34 ± .06 (mean ± standard error), and 1.27 ± .04 for post-stimulus injection. In trials using alarm pheromone, the mean index value for pre-stimulus injection was 1.28 ± .02 , and 1.99 ± 0.23 for post-stimulus injection. The first six trials performed in our experiment used DI water stimulus, and mean temperature for these trials was 11.1°C, while the subsequent 12 trials using the alarm pheromone stimulus had a mean temperature of 7.3°. Our pheromone treatments occurred at lower ambient temperatures than our DI water treatments (t_{12} = 6.76, p = $1.992e^{-5}$), and fish in these treatments exhibited greater responses to direct predation risk than in higher temperature trials.

In our alarm pheromone treatments, the introduction of alarm pheromone increased the mobility of stickleback groups in the tank. Whereas during pre-trial acclimation periods and pre-stimulus periods during trials fish were frequently stationary in loose groups, the alarm pheromone

seemed to create a fright response causing groups of sticklebacks to move around the tank. Fish also occurred predominantly in one group during trials, and only in one were fish observed in multiple groups. In one trial, fish were observed in three distinct groups immediately after the introduction of the alarm pheromone, but this lasted only briefly and the three groups merged in to one almost immediately. Contrary to alarm pheromone treatments, introduction of DI water to the tank seemed to elicit no response from fish at all, and little to no movement/perceived fright response occurred in these trials.

Hydroacoustic Surveys

For our analysis, sample size (n=21) was low compared to the total number of schools detected through the course of our four surveys (n=53). We had to remove substantial portions of our data due to recurring difficulties associated with the ship-born GPS system interface with our acoustic data recording software. Our echosounder was able to accurately determine the vertical linking distance of schools (school height), as this is calculated based solely on the properties of the acoustic beam, but calculating horizontal linking distance (school width along the horizontal plane) required GPS functionality and we subsequently removed 32 schools observed during periods of GPS malfunction from our analysis (**Table 2.6**). Detection rates of schools (from the cumulative n=53 sample) did not differ between active (0.32 schools/km) and fallow (0.27 schools/km) farm sites ($t_{40} = 0.25$, $p = 0.80$).

We tested for differences in school size (biomass) and vertical stratification between active and fallow farm sites. School size estimates are reported as NASC, and vertical stratification is reported as a ratio quantity between school length and school height to mitigate any effects of group size that may have biased measurements in the vertical dimension alone. We found no

differences in school size between control and treatment sites ($t_{15} = 0.95$, $p = 0.356$), but schools in fallow bays (n=10) were significantly more stratified in the horizontal dimension than schools in active bays (n=11) ($t_9 = 3.54$, $p = 0.005$) (**Figure 2.5**). Average ratio length:height of schools in fallow bays was 6.37, and 1.09 for schools detected in active farm bays. More specifically, within fallow bays average school height was 3.9m and these schools were horizontally dispersed over a mean distance of 22 meters. Conversely, height of schools in active bays averaged 3.24m, but were only horizontally dispersed over a mean distance of 3.6m.

Discussion

Our results show that high risk of encountering a predator caused changes in the aggregative behaviors of marine pelagic fish schools. We showed that risk effects are directly quantifiable in a lab setting, and were able to obtain field data showing that the behavioral signals generated by marine pelagic fish schools may be a potential barometer for measuring the effects of predation risk on the structure of these ecosystems.

In our lab experiment, we measured the 2-dimensional aggregative properties of stickleback groups using the index of dispersion to determine the relative impact that environmental and direct predation risk have on group structure. We detected no differences in aggregative behaviors of stickleback groups due to the effects of environmental risk, but groups from both hunger treatments exposed to the effects of alarm pheromone formed tighter groups than groups in DI water treatments, suggesting that, group behavior is most sensitive to the effects of direct predation risk, despite a lack of statistical significance ($p = 0.057$ for alarm pheromone treatments). Hoare et al. (2004) also found that in a laboratory setting, groups of banded killifish (*Fundulus diaphanous*) formed larger schools in response to alarm pheromone

exposure than in treatments where they were exposed to olfactory cues indicating food availability. However, groups in this experiment were only comprised of a few individuals (<10) and in marine environments where fish schools can exceed several million individuals (Misund 1993), increases in group size have only marginal antipredator benefits for individuals within the school (see Rieucau et al. 2015), while changes in school morphology may be more effective behavioral adaptations to direct predator encounters (Nøttestad et al. 2002; Axelsen et al. 2001; Nøttestad & Axelsen 1999; Nøttestad et al. 1996). As well, although temperatures differed significantly between DI water and alarm pheromone treatments, we were able to control for temperature effects by analyzing changes from pre- to post-stimulus conditions within individual trials. However, with respect to potential temperature effects, our results agree with Pink & Abrahams (2018) who showed that the impact of predation risk is directly affected by temperature where lower temperatures reduce activity levels of fish and consequently increase the effects of predation risk. Higher temperatures lead to higher basal metabolic rates, and forgoing feeding opportunities therefore increases risk of starvation. For foraging fish, this consequently results in a reduced response to predation risk.

In our field data, we found no difference in group size between active and fallow farm sites. The relatively homogeneous size-distribution of schools across the larger spatial landscape may reflect a mismatch between actual and perceived predation risk by fish schools (Gaynor et al. 2019), where airing on the side of caution (occurring in larger-than-necessary group sizes) may lead to higher survival rates (Bouskila & Blumstein 1992) for individual fish. Ioannou et al. (2008) showed that the size and number of groups has significant effects on predators' ability to detect and locate individual schools, and homogeneous school sizes across the larger spatial environment may also reflect adaptations to predation risk present at this scale. Our subsequent

analysis of school morphological parameters showed that schools around active sites were more vertically stratified than counterparts at fallow sites, which occurred in discoid shapes. Schools in fallow bays may have been utilizing the benefits of hydrodynamic efficiency associated with discoid school morphologies (Abrahams & Colgan 1985), whereas the higher vertical stratification of schools detected around active sites may confer comparatively higher predator detection capabilities. There does exist the potential that cues from caged salmon may be eliciting behavioral responses from wild counterparts. However, it is likely that wild fish have become habituated to these cues, as they are likely provided out of context by caged fish. If skin extract cues are present in the environment from farm salmon in cages, they are not necessarily an indicator of potential mortality risk as caged fish pose no risk to wild counterparts outside of cages, nor are the cues necessarily indicative of an approaching or attacking predator as ranched salmonids have significantly reduced responses to predators (Biro et al. 2004). Cues from farm fish therefore have no context, while cues from wild predators have ecological context in the form of mortality risk.

Although length:height ratios showed significantly higher vertical stratification in active bays, height values when measured independent of school length were actually higher in fallow than in active bays (3.94 to 3.24m respectively). Coupled with the large disparities in horizontal dispersion between schools at fallow and active sites (22.54 to 3.63m respectively), this would suggest significant differences in school packing (density) given the lack of difference we observed in NASC values that were also observed. These results match predictions from our lab experiment, where fish exposed to simulated predator encounters (pheromone extract) formed tighter groups than fish exposed to DI water stimulus. In our field data, active farm sites constitute high risk due to the attraction of larger predators that feed on smaller fishes (Serra-

Llinares et al. 2013), and densely packed schools are an advantageous antipredator strategy allowing fish to coordinate evasive maneuvers based on direct and potentially lethal predator attacks (Pitcher et al. 1996). These comparative results show that the behavioral metric used to detect responses to predation risk in the lab can be utilized as a means to interpret field data collected at spatial scales far exceeding those possible in a laboratory setting. In this light, preexisting knowledge of behavioral responses to predation risk, such as those present within literature on fish school—predator dynamics, may provide avenues for researchers to measure the magnitude to which predation risk affects the behavior of animals at large spatial scales if the appropriate analysis metrics can be properly identified.

The effects of predation risk on ecosystem structure are well known in terrestrial and aquatic environments (Ripple & Beschta 2004; Werner et al. 1983). Animals utilize the features of their environment to control predation risk (Schmitz et al. 2008; Wirsing et al. 2007), and the magnitude to which predation risk influences animal behavior is therefore in part determined by the physical environment. Research from coastal marine systems has showed that physical habitat complexity allows prey animals to tolerate increased exposure to predators without subsequent increases in mortality rates (Heithaus et al. 2009; Wirsing et al. 2007), but marine pelagic fishes are unable to rely on analogous mechanisms and instead must rely on behavioral mechanisms such as schooling.

In marine pelagic environments, schooling is a commonly observed behavioral strategy with known anti-predator (Rieucau et al. 2015) and foraging benefits (Pitcher et al. 1986) for pelagic fish. Pelagic schools can experience a predatory regime with highly variable feeding capacities (e.g. whales capable of consuming an entire school of fish in one attempt versus smaller fish predators capable of removing only one individual per attack attempt), and

behavioral responses to direct encounters with predators therefore vary with respect to different feeding capabilities and hunting strategies of the attacking predator(s) (Nøttestad et al. 2002; Nøttestad & Axelsen 1999; Nøttestad et al. 1996). However, these direct encounters with predators constitute only a portion of the cumulative effect of predation risk, and the fear of being preyed upon is also an important influence on animal behavior. Research in marine systems has focused on understanding the strength of fear-driven effects ('landscape of fear') (Gaynor et al. 2019; Catano et al. 2017; Catano et al. 2016), yet these studies occur primarily in coastal systems with comparatively higher levels of physical habitat heterogeneity than pelagic counterparts. Applying behavioral principles gleaned from these studies to pelagic systems is therefore difficult due to differences in habitat characteristics between coastal and pelagic marine ecosystems.

Human activities in marine environments can introduce small patches of physical structure that have strong aggregative effects on wild fish. Fish aggregation devices (FADs) are common in pelagic fisheries, and aggregate wild fish that would otherwise be too widely dispersed for fisheries to efficiently locate and capture (Noranarttragoon et al. 2013). Aquaculture sites have analogous attractive effects on pelagic fishes that have been documented on both sides of the Atlantic. Aggregations around farm sites have been described within the context of species composition (Dempster et al. 2004), dietary effects resulting from the consumption of excess farm feed (Dempster et al. 2011), and reproductive fitness of farm-associated fish (Barett et al. 2018), and Dempster et al. (2009) described this as an 'ecosystem-level' effect. Despite this recognition that the effects of active aquaculture potentially span entire ecosystems, little focus has been placed on quantifying the spatial extent of the aggregative effect generated by these sites (but see Machias et al. 2005; Goodbrand et al. 2013). Where

pelagic animals are often highly mobile and widely dispersed and the ecosystems they occupy are riddled with logistical constraints for researchers, aquaculture sites affect the structure of these ecosystems by aggregating animals in relatively small spatial areas. We were able to utilize these aggregations as a source of data, and were successfully able to show that behavioral principles used to study predation risk in a laboratory setting can be applied in the field to study the effects of marine pelagic predators on ecosystem structure at large spatial scales.

Our understanding of how risk effects aggregation behavior of fish in marine pelagic ecosystems has predominantly been developed using multibeam acoustics (see Benoit-Bird & Lawson 2016 for review) that rely on continuous observations of individual schools during encounters with predators. Despite the effectiveness of this approach in quantifying direct risk effects, multibeam acoustics are relatively limited in their ability to quantify behavioral patterns at larger spatial scales, and multi-frequency acoustics have been a useful tool in describing the dynamics of group behavior in response to different environmental factors at these scales in pelagic environments (Jech et al. 2012, Nakamura & Hamano 2009). In our study, we were successfully able to use a split-beam acoustic system to describe the behavior of pelagic fish schools, and identify behavioral patterns indicative of risk effects without making any direct observation of predators. We took an approach similar to Bleicher et al. (2019) where instead of asking 'what can predation risk tell us about animal behavior?' we asked 'what can animal behavior tell us about predation risk?' We treated different components of school dynamics (size and morphology) as a form of behavioral language, and were successfully able to identify differences in this behavioral language between fish schools around aquaculture sites with predictable risk levels, showing that we can use the dynamics of fish school behavior to quantify spatial gradients in predation risk. As well, although we were unable to perform hook-and-line

surveys to determine the species composition of the schools on our echograms, single-species schools are rare and difficult to observe acoustically (Trenkel et al. 2008), and results from Paramo et al. (2010) show that environmental factors are stronger determinants of group dynamics than species identification and life stage.

Apex predators are important facets of nearly every healthy ecosystem on earth, and understanding the life history of these animals is an important component of our understanding of ecosystem structure. Examples from pelagic marine ecosystems include tunas, dolphins, whales, orcas, swordfish, marlin, and many others. Some of these predators have substantial commercial value, and fishermen regularly remove a significant percentage of large predator populations in marine pelagic ecosystems every year (Pauly et al. 1998). Management of these populations is difficult because the study of apex predators is often restricted by logistical and financial difficulties. The use of behavioral data from more accessible animals such as schooling pelagic fish species from which risk levels can be assessed may provide additional data to supplement our understanding of how apex predators affect the structure of pelagic marine ecosystems.

Although these predators have a large impact on the structure of the pelagic risk environment, anthropogenic activities like fishing may have a substantially larger impact than we are currently aware (see Heithaus et al. 2008). Therefore, understanding the true magnitude of this effect requires a better understanding of how predators influence the structure of prey populations through consumptive and non-consumptive effects. Although scientists have only recently utilized hydroacoustic systems as a source of behavioral data, commercial fishermen have relied on hydroacoustics for decades as a means of effectively locating and capturing target species. Our data, along with data from other studies using hydroacoustic systems to study fish

behavior, may therefore elicit potential as a means to mapping the effects of predation risk on the structure of marine pelagic ecosystems. Commercial vessels equipped with hydroacoustic systems are a potential source of data that may be used to develop to deeper understanding of the spatial and temporal variations in the marine pelagic risk environment, and how this variation contributes to ecosystem structure.

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Figures & Tables

Table 2.1. Trial information from our laboratory experiment. All temperatures were maintained at ambient, and risk treatments indicate the combination of hunger treatment and experimental stimulus (alarm pheromone or distilled water).

Trial	Risk Treatment	Temperature
1	Satiated + DI Water	11.3
2	Starved + DI Water	11.2
3	Satiated + DI Water	11.2
4	Satiated + DI Water	11.2
5	Starved + DI Water	11.2
6	Starved + DI Water	10.5
7	Satiated + Alarm Pheromone	10
8	Starved + Alarm Pheromone	9
9	Starved + Alarm Pheromone	10
10	Satiated + Alarm Pheromone	8.4
11	Starved + Alarm Pheromone	8.4
12	Satiated + Alarm Pheromone	7.4
13	Starved + Alarm Pheromone	7.3
14	Satiated + Alarm Pheromone	6.6
15	Satiated + Alarm Pheromone	5.4
16	Satiated + Alarm Pheromone	5.4
17	Starved + Alarm Pheromone	4.4
18	Starved + Alarm Pheromone	5.4

Table 2.2. Active/Fallow bays between years. Old Woman Cove, Little Burdock Cove, and Mal Bay were not surveyed in 2016, 2014, and [Fall] 2015, respectively, due to logistical difficulties, and Salmonier Cove, Red Cove, Murphy's Cove, and Harbor Breton were not surveyed in 2014 due to limitations in our survey plan.

	Survey			
Site Name	**Fall 2014** (Sept 17-19)	**Spring 2015** (July 28-31)	**Fall 2015** (Oct 5-9)	**Fall 2016** (Sept 19-23)
Poole's Cove	Active	Active	Active	Fallow
Hickman's Point	Active	Active	Active	Fallow
South East Bight	Active	Active	Active	Fallow
McGrath Cove	Active	Active	Active	Fallow
Old Woman Cove	Active	Active	Active	*not surveyed
Deep Water Point	Fallow	Active	Active	Active
Little Burdock Cove	*not surveyed	Active	Active	Active
Rencontre Island East	Fallow	Active	Fallow	Active
Mal Bay	Active	Active	*not surveyed	Active
Ironskull	Fallow	Fallow	Active	Active
Salmonier Cove	*not surveyed	Active	Fallow	Active
Red Cove	*not surveyed	Fallow	Fallow	Fallow
Murphy's Cove	*not surveyed	Fallow	Fallow	Active
Harbor Breton	*not surveyed	Active	Active	Active

Table 2.3. Echosounder settings used during each of our surveys. Echosounder calibration occurred immediately prior to each of our surveys using the standard tungsten-carbide sphere method.

Device Settings	Echosounder
Type	Simrad EK60
Beam Characteristic	Split Beam
Frequency	38kHz
Individual Beam Angle	6.98°
Pulse Length	1.024ms
Pulse Rate	$1s^{-1}$
Transmission Power	2kW
Time Varied Gain	20LogR
Range	Variable

Table 2.4. Number of transects as well as sampling effort allocated to each of our survey bays across our four surveys. Number of transects within a respective bay was determined by bay area relative to total area sampled with the minimum number of transects in any one bay being 3. Values of 'NA' indicate that the respective bay was not surveyed during that cruise. Asterisks indicate the loss of transect data due to technical difficulties with our onboard recording system.

	Number of Transects					Distance Sampled (km)			
Site Name	**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**		**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**
Poole's Cove	9	11	12	9		14.232	17.659	18.159	13.629
Hickman's Point	6	7	7	7		8.454	10.887	10.928	10.078
South East Bight	3	3	3	3		1.992	1.949	2.012	2.321
McGrath Cove	3	2*	3	3		2.94	1.44*	1.963	2.185
Old Woman Cove	6	2*	3	NA		2.42	0.539*	1.05	NA
Deep Water Point	4	3	4	3		3.851	2.486	2.557	2.632
Little Burdock Cove	NA	3	4	3		NA	1.484	1.67	0.912
Rencontre Island	3	3	3	3		2.416	1.732	1.836	1.33
Mal Bay	9	5	NA	5		7.83	4.492	NA	4.242
Ironskull	6	5	5	5		6.635	4.487	3.917	4.405
Salmonier Cove	NA	3	3	3		NA	1.915	1.51	1.997
Red Cove	NA	3	3	3		NA	1.613	1.374	1.849
Murphy's Cove	NA	7	6	4		NA	7.418	5.847	4.336
Harbor Breton	NA	15	15	17		NA	13.999	11.319	10.971

Table 2.5. Schools detection module settings used in analysis of fish schools detected in hydroacoustic surveys. The same settings were used for analysis of data from all four surveys.

Device Settings	Module Detection Settings
Minimum Detection Threshold	-70dB
Maximum Detection Threshold	0dB
Minimum Total School Length	2.0m
Minimum Total School Height	2.0m
Minimum Candidate Length	2.0m
Minimum Candidate Height	2.0m
Maximum Vertical Linking Distance	5.0m
Maximum Horizontal Linking Distance	5.0m

Table 2.6. Schools data removed from each of our four surveys. Schools were removed from our analysis because of GPS failures that prevented our on-board recording device from calculating horizontal length of schools.

Survey	**Schools$_{removed}$**	**Schools$_{good}$**	**Schools$_{TOTAL}$**
Fall 2014	1	7	8
Spring 2015	19	0	19
Fall 2015	10	13	23
Fall 2016	2	1	3
TOTAL	32	21	53

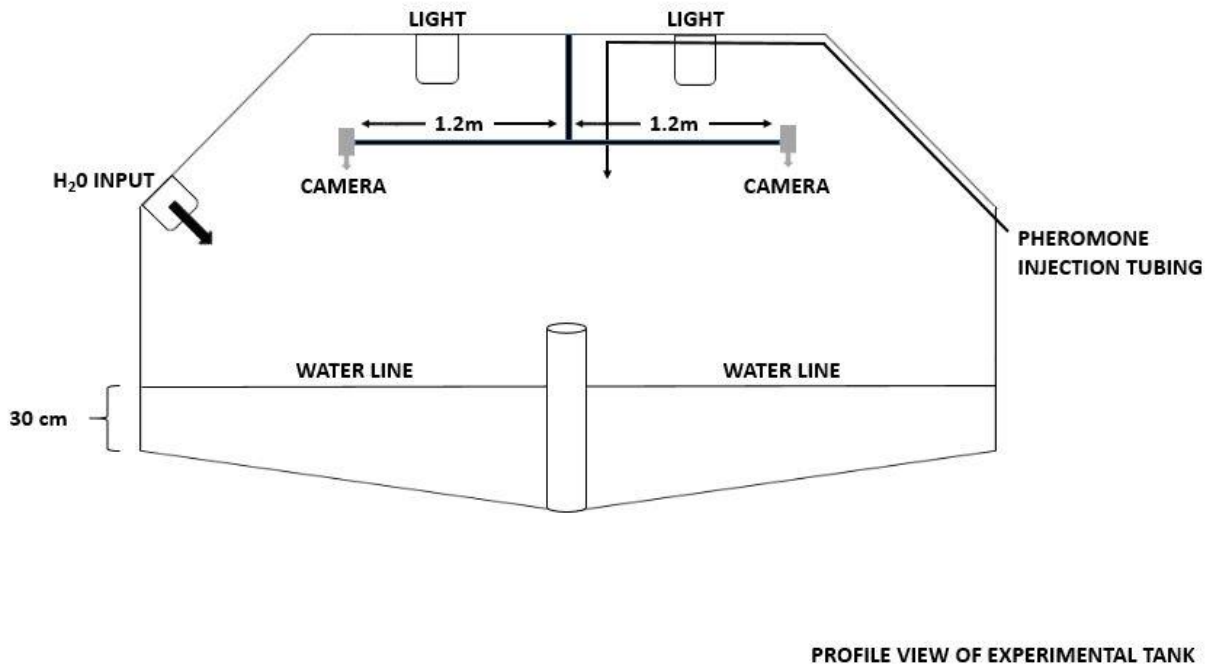

Figure 2.1 Profile view of experimental tank (total diameter: 4.8m). Through the course of all acclimation periods and experimental trials, the tank was covered with an opaque black tarp to limit any effects of external stimuli on fish behavior. Cameras were suspended two meters above the bottom of the tank and for each, the field of view encompassed half of the tank area. Pheromone injection tubing was attached to the underside of the opaque tarp and used to manually injected the experimental stimulus at the midpoint of each trial without disturbing fish in the tank. Total volume of the experimental tubing was 50mL, and prior to each trial the stimulus was injected in to the tubing, and flushed in to the tank at the 10 minute marker of each trial through the tubing via displacement using an additional 50mL of distilled water.

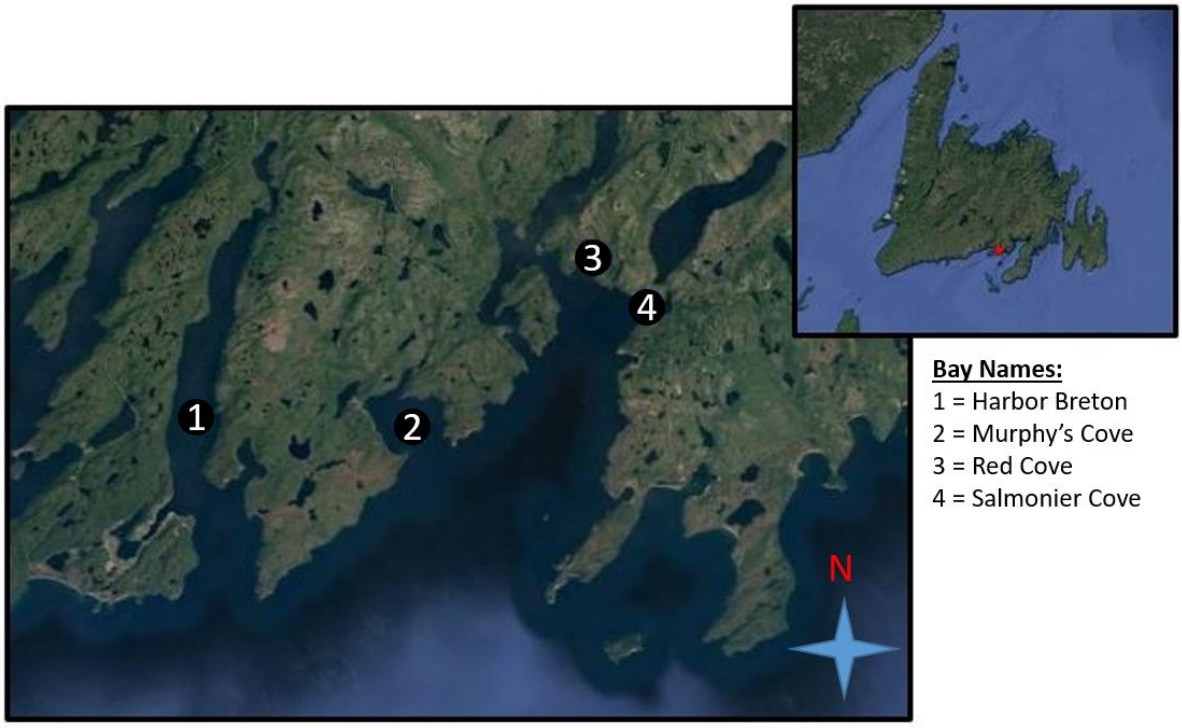

Figure 2.2. Survey bays located in the Harbor Breton area. Targeted bays are indicated with numbers. Bays indicated with numbers were surveyed only for 2015 and 2016 cruises. Harbour Breton (western-most survey location) and Red Cove (Northern-most survey location) were only surveyed during active and fallow periods respectively for 2015 and 2016 surveys. The remaining two sites (Murphy's Cove and Salmonier Cove, west to east) were surveyed during both active and fallow periods for 2015 and 2016 surveys.

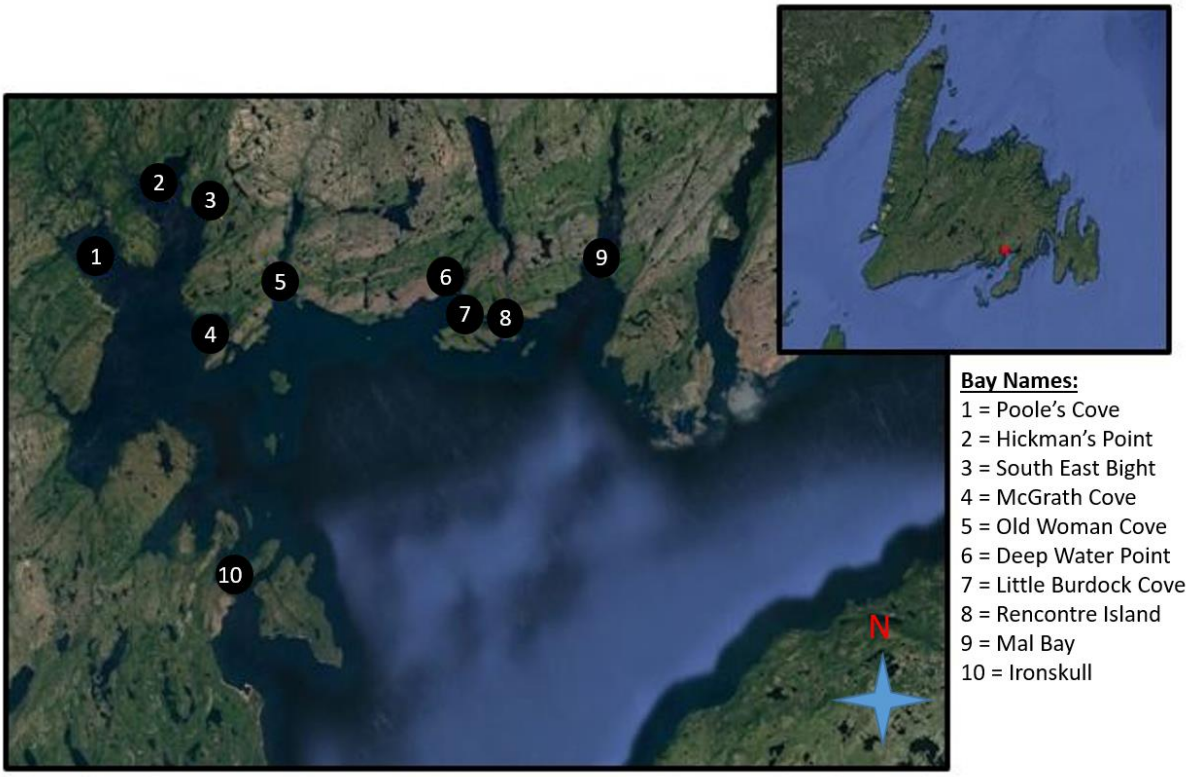

Figure 2.3. Survey bays located in Fortune Bay. Targeted bays are indicated with numbers. All but three bays were surveyed during active and fallow periods for all 2014, 2015, and 2016 surveys. Little Burdock Cove and Mal Bay were not surveyed in 2014 and [Fall] 2015, respectively, and Old Woman Cove was not surveyed in 2016 due to logistical difficulties. Each of these three bays were only surveyed during periods of active farm production.

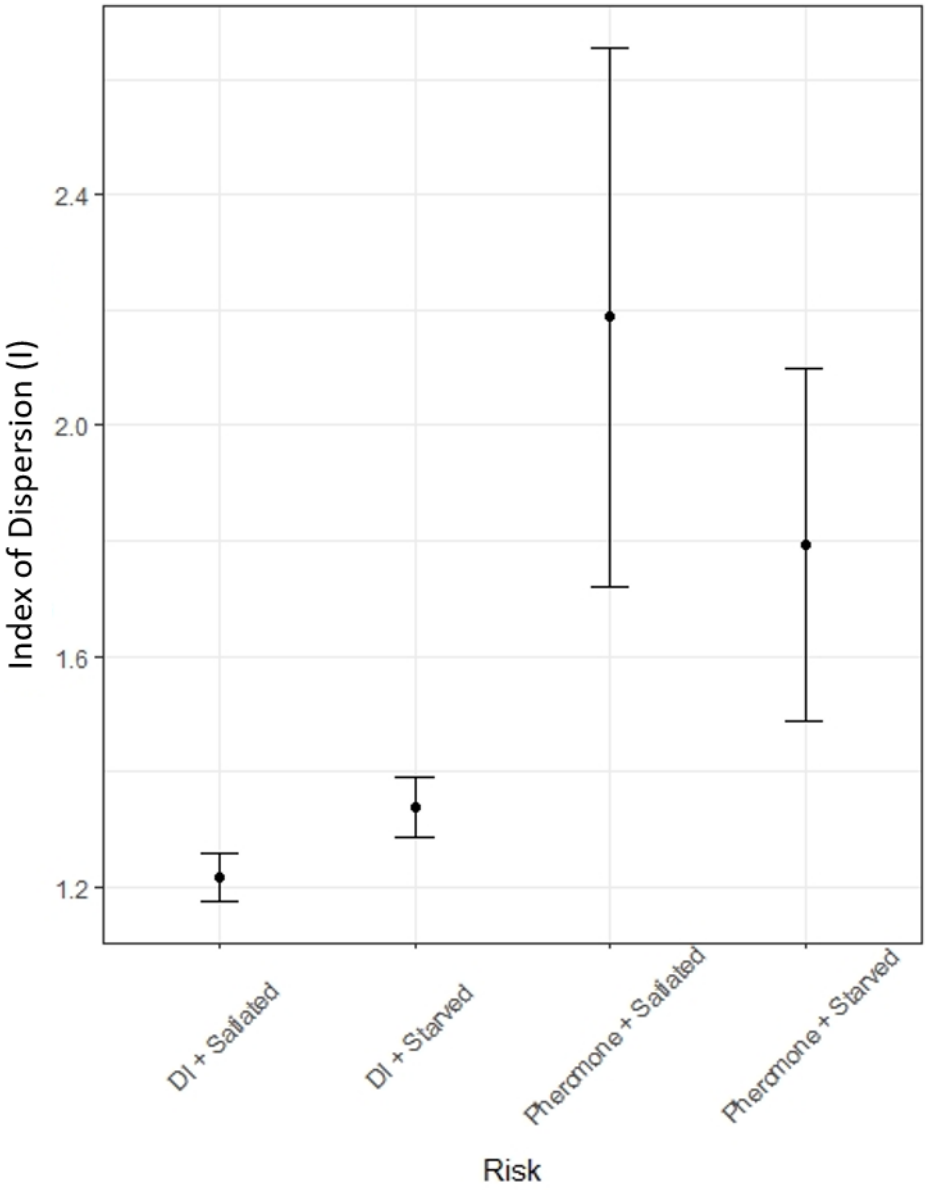

Figure 2.4. Index of Dispersion (I) values from post-stimulus periods. Categories on the x-axis represent experimental treatments ('DI' refers to distilled water treatments) with error bars showing ± 1 standard deviation from the mean. Index values of 1 indicate a random pattern, values > 1 indicate clumped patterns, and values approaching zero indicate uniform patterns.

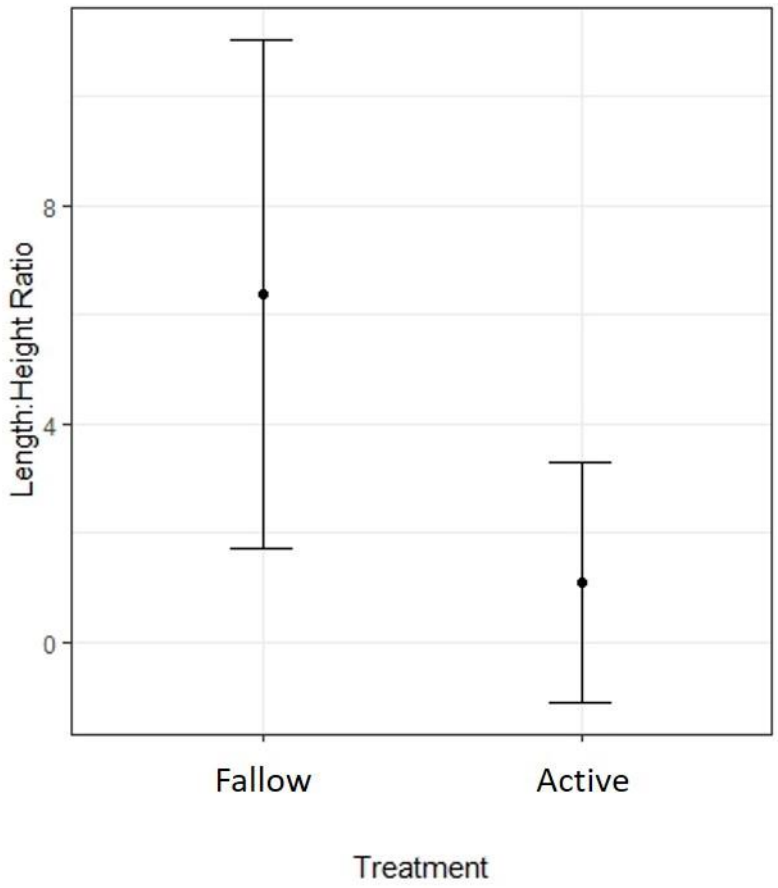

Figure 2.5. Length:Height ratio of schools in active and fallow aquaculture bays. Error bars are ± 1 se from the mean, and all school measurements were made in meters (m). Repeated GPS failures resulted in the removal of significant numbers of schools (n=32) from our analysis, resulting in a final sample size of n=21. Ten schools (n=10) from fallow bays and eleven schools (n=11) from active bays are depicted in the plot.

Chapter 3. Marine aquaculture operations affect predator distributions and fish school dynamics at large spatial scales

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Abstract

Ecosystem structure is defined by the combination of top-down and bottom-up processes. Particularly with respect to predation risk, our understanding of the ecological drivers underlying these processes has largely been from terrestrial systems, while marine environments have received comparably less attention. Rapid human ingression into marine environments, however, necessitates that further research be undertaken to better understand the effects of these anthropogenic activities on the structure and function of the ecosystems they directly interact with. Marine aquaculture attracts wild organisms at larger spatial scales than previously documented due to spatiotemporally predictable resources (food and structure) available to wild pelagic organisms, yet the overarching ecological effects of this phenomenon remain understudied. Visual observations of large predators and hydroacoustic survey data were used to describe effects of sea cage aquaculture on the spatial distribution of predators and the subsequent effects on the behavior and distribution of schooling fishes around aquaculture farms. Predators were observed exclusively around active aquaculture sites, and schools of fish found in these locations were significantly more vertically stratified than counterparts from areas with inactive sea farm sites, suggestive of increased vigilance toward predators. Collectively, our results show a multi-trophic aggregative effect caused by farm activity, and that the increased abundance of predators around active farm sites is reflected in the morphological dynamics of fish schools at these locations.

Introduction

Ecosystems are governed by top-down and bottom-up forces that are a consequence of animals competing for food while avoiding being a meal for something else. For that reason, a substantial body of work has been devoted to understanding the relative impact that food and predators have on ecosystem structure, and has shown that animals make behavioral decisions by weighing risk against potential rewards associated with that decision (Brown et al. 2004; Werneret al. 1987; Werner et al. 1983). Behavioral ecologists have traditionally treated food as the currency to understand behavior, and have shown that the effects of top-down control (predation risk) are impacted by a wide range of variables, including an animal's energetic state (Alonso 2002; Houston & McNamara 1988), the physical environment (Werner et al. 1983), and an animal's perceived ability to reduce its probability of being consumed by a predator (Schmitz et al. 2008). However, research focus on terrestrial systems far supersedes that given to aquatic and marine systems (Menge et al. 2009), leaving a comparatively underdeveloped understanding of the ecological forces in marine environments.

In terrestrial environments, population dynamics and community structure play an important role in dictating ecosystem structure, whereas the structure and function of marine communities is affected comparatively more by physical processes (Steele 1985). Much of the ocean is dominated by a structurally uniform pelagic habitat, whereas terrestrial ecosystems are comparatively more structurally heterogeneous. The vertical dimension in marine environments also allows animals to exploit resources over vertical and horizontal spatial gradients (Certain et al. 2011; Benoit-Bird & Au 2003), and the application of two-dimensional terrestrial landscape ecology principles to pelagic marine ecosystems is therefore difficult (Wedding et al. 2011). The

open ocean is also subject to human activities which may be having a significant impact on the structure of these ecosystems in conjunction with biological processes (Madin et al. 2016).

Human activities influence marine environments positively (e.g., by creating resource patches for wild animals, Dempster et al. 2009; Tuya et al. 2006), and negatively (e.g., by removing large quantities of animals from the world's oceans every year, FAO 2018). The increasing rate of human ingression into marine environments is affecting ecosystem structure (Steneck et al. 2004), and our understanding of top-down and bottom-up processes is therefore contingent on our ability to account for both natural and anthropogenic forces that effect these processes (Heithaus et al. 2012; Certain et al. 2011; Heithaus et al. 2008). Human activities create levels of environmental predictability at spatial and temporal scales that are rare in natural systems (e.g., estuaries, polynyas, upwelling zones, thermoclines, and turbidity fronts), and given the natural relationship between variability and scale (Levin 1992, **Figure 3.1**), these activities can create novel resources that are predictable at fine spatial and temporal scales. One example are sea cage aquaculture sites. They are known to attract significant amounts of wild animals (Dempster et al. 2009; Boyra et al. 2004; Dempster et al. 2004) at large spatial scales (Goodbrand et al. 2013) that consume excess feed from cage feedings (Dempster et al. 2011).

Sea farms compress the spatial and temporal variation in food availability for marine predators. Aggregations of wild fish found around pelagic sea farms reduce the need for these predators to invest in search behavior because these aggregations persist through time at predictable locations (Dempster et al. 2004). Where many pelagic predators exploit patterns in food availability across substantial spatial scales (e.g. Richardson et al. 2016), patterns in top-down ecosystem control created by these movements may change substantially when predators know exactly where and when to find food. Our mechanistic understanding of pelagic ecosystem

structure is already lacking in comparison to terrestrial systems, and because human activities like aquaculture are rapidly expanding in these environments, it is important to understand how these activities are changing the structural components of the ecosystems they occupy (e.g. Madin et al. 2016).

In this paper, we investigate how sea cage aquaculture effects the magnitude of top-down processes in pelagic marine ecosystems. These environments are typically defined by a lack of physical structure, and the outcome of predator-prey interactions is likely contingent on behavioral mechanisms developed to control risk or increase foraging efficiency (for prey and predator respectively). Sea cages in pelagic environments provide wild fish with both food (Dempster et al. 2011; Fernandez-Jover et al. 2011) and artificial structures in the form of cage infrastructure, and the combined effects of food and structure likely contribute significantly to the aggregative effect of sea farms. Studies clearly show that fish aggregations around farm sites persist through time (e.g. Machias et al. 2005), but it is unclear how predators alter their behavior to contend with a spatially and temporally predictable prey source whose behavior is dictated by a point-source effect rather than by natural variation in food availability. Our goal is therefore to determine the relative abundance of predators around active and fallow farm locations, and determine how the behavior of these predators affects prey species.

Methods

Schooling is an important anti-predator behavior in fish (Magurran 1990), and changes in school structure in response to predation risk have been well documented in pelagic fish (Rieucau et al. 2015; Nøttestad et al. 2002; Axelsen et al. 2001; Nøttestad & Axelsen 1999; Nøttestad et al. 1996; Fréon et al. 1992). In the second chapter of this thesis, we also showed that school structure is an efficient barometer for the risk environment, and may be used to distinguish

between habitats with different endemic risk levels. School size also effects predator encounter rates (Ioannou et al. 2011), and we used hydroacoustic data to compare the biomass and external morphology of fish schools between control and treatment sites as an indirect measure of relative predator abundance. In this study, we also calculated the proximity of predator sightings to both active and fallow aquaculture bays to determine if active aquaculture sites were influencing foraging behavior of pelagic predators. Expected schooling species include Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and capelin (*Mallotus Virens*). Likely predators include Blue sharks (*Prionace glauca*), tuna sp., orcas (*Orcinus orca*), dolphin sp., and whales.

Hydroacoustic Surveys

Hydroacoustic surveys were conducted using our 10m dedicated hydroacoustic research vessel the RV Gecho II. This vessel was equipped with a Simrad EK60 38/120kHz split-beam transducer **(Table 3.1)** which was calibrated prior to each survey using a standard tungsten-carbide sphere. On the port side of the vessel, our transducer was mounted on a winch system which made for easy deployment and retrieval. Data were recorded directly on ship-board computer systems and as well viewed live on our vessel's computer system.

We performed four hydroacoustic surveys, one in September 2014, July 2015, October 2015, and Sept 2016, respectively, at Atlantic salmon (*salmo* salar) aquaculture sites on the south coast of Newfoundland from Harbour Breton (47°28'23" N, 55°50'06" W) through Fortune Bay (47°35'49" N, 55°24'32" W) (**Table 3.2**). Cumulatively, 14 different bays containing active or fallow Atlantic salmon aquaculture sites were surveyed, where active sites contained between 8 and 24 circular net-pens, each 10m diameter and approximately 20m deep. Active farm sites also

contained different age-classes of salmon, from post-smolt to adult, and different age classes were segregated between bays. Our surveys took place over a three-year period, and 9 of 14 bays were surveyed during active and fallow periods (between surveys) due to the timing of fish stocking/harvesting. During fallow periods, cage infrastructure is largely removed from the water, with the exception of intermittent periods post-harvest where barebones cage infrastructure (i.e. cage without netting) remained in the water, but were subsequently removed for the duration of the fallow period.

Sampling effort devoted to each bay was based on bay area relative to total area sampled (**Table 3.3**), and we utilized a randomized transect design within each survey bay. The aggregative effect of sea farms in this area occurs at large spatial scales (Goodbrand et al. 2013), and we subsequently allocated survey efforts to the entire bay rather than only the immediate vicinity of the net pens (individual bays constitute independent observations). Because bays varied significantly in size, the minimum number of transects performed in any bay was 3 (**Table 3.3).** All transects were run between 5-7 knots parallel to the entrance of the respective bay, with transect locations were randomly selected based on the total number of non-overlapping transects possible as a function of bay area and acoustic beam width. For smaller bays. Due to technical difficulties, two transects from our Spring 2015 survey were unusable (see **Table 3.3**). In these two instances, only 2/3 of the planned transects were used in our analysis.

Echoview software (version 7.0.97) was used to process our data, and we used the schools detection module to obtain estimates of school parameters used in our behavioral analysis (**Table 3.4**). The importance of school structure as an antipredator mechanism have been well documented in pelagic fish (see Rieucau et al. 2015), and variation in school morphology effects predator detection capabilities and hydrodynamic efficiency of individuals

within the school (Daghooghi & Borazjani 2015; Abrahams & Colgan 1985). We used vertical stratification as a proxy measure for vigilance and predicted that schools in active bays would be more vigilant towards predators than in fallow bays. Schools of fish have been shown to sacrifice hydrodynamically efficient discoid structures in favor of increased vertical stratification in response to predator presence, and we therefore considered comparative degrees of vertical stratification between schools in active versus fallow bays to be indicators of predator-induced risk effects (see Abrahams & Colgan 1985). Vertical stratification was quantified using the length—height ratio of observed schools, as school size may bias vertical measurements if a correction factor is not applied. Where Goodbrand et al. (2013) examined the distribution of biomass between active and fallow sites in a binary fashion (comparing active vs. fallow bays), we gradated our survey bays by time spent within the current activity status (active or fallow), and activity status was therefore on a continuous scale allowing for comparison of vertical school stratification using linear models to account for relative time spent in active and fallow states. We also tested for differences in school biomass between active and fallow bays to ensure that any potential differences in the structural parameters were not a consequence of differences in group sizes. Biomass estimates are reported using the nautical area scattering coefficient (NASC) (see MacLennan 2002).

Predator Sightings

We surveyed a total of 35 active and 14 fallow aquaculture bay periods. Active sites outnumbered fallow sites on all four of our surveys, and 74.4% of our survey effort (99.14km total distance sampled) therefore occurred in active bays while 25.6% (34.31km total distance sampled) occurred in fallow bays. Sightings only occurred along acoustic transect lines for our

hydroacoustic survey data, and sampling distance relative to bay status is therefore the same as that presented in our hydroacoustic data. We calculated the number of active and fallow bays within a 3km radius of predator sightings to determine if predators were selectively allocating foraging effort between active and fallow sites (mean distance between adjacent survey bays was 3km). We treated individual bays as observational units based on the scale of aggregative effect demonstrated by Goodbrand et al. (2013).

Large piscivorous predators were visually observed with the naked eye in eight independent instances during our hydroacoustic surveys (**Table 3.5**), and two sightings also occurred in Little Passage, Bay D'espoir, NL (47°38.649' N; 55°55.432' W) during an independent portion of our survey. Predator observations were exclusively visual (naked-eye or binoculars) and therefore reliant on predators breaching the surface water (we did not detect any large predators using our hydroacoustics). However, we were also able to detect demersal predators (likely Cod, *Gadus morhua*) but unable to specifically measure the abundance of these individuals due to limitations in our analysis software. Cod most often appeared as individual fish targets within our echograms and in analysis of these targets required the use of a software module that was unavailable to us.

Results

Hydroacoustic Surveys

We analyzed 133.45 nautical miles of transect data from our four surveys and detected a total of 53 schools; 12 in fallow bays and 41 in active bays. Despite the disproportionate allocation of sampling effort between active and fallow sites, detection rates of schools (from the cumulative n=53 sample) did not differ between active (0.32 schools/km) and fallow (0.27 schools/km)

farm sites ($t_{40} = 0.25$, $p = 0.80$). Although our total sample size consisted of n=53 schools, recurring GPS malfunctions resulted in the loss of large quantities of metadata necessary for data processing, and we were therefore only able to incorporate 21 of the 53 observed schools in our analysis (11 from active bays, 10 from fallow bays). GPS functionality is required for horizontal measurements of school structure, and although several attempts were made at remedying recurring problems, we were unable to do so. Our biomass estimates were not affected by GPS malfunctions, as NASC is calculated by averaging beam properties over 1nm sampling units, and we were able to use all schools (n=53) in this analysis.

We tested for differences in vertical stratification using activity status as our predictor variable, and found that schools detected in bays with longer periods of active farming were increasingly more vertically stratified than their counterparts detected in fallow bays ($F_{1,19} = 19.85$, $p = 0.00027$) (**Figure 3.2**). Average length:height of schools in fallow bays was 6.37:1, and 1.09:1 for schools detected in active farm bays. Average school height in fallow bays was 3.9m, and average horizontal dispersal was 22 meters. In active bays, school height averaged 3.24m, and mean horizontal dispersal was 3.6m. We also tested for differences in the biomass of schools between active and fallow bays (also using activity status as our predictor variable) to ensure that school size was not affecting our results, and found no differences between control and treatment sites ($F_{1,19} = 0.312$, $p = 0.583$) (**Figure 3.3**). Although NASC estimates were available for all 53 individuals, the analysis presented in Figure 3.3 uses the same subsample of n=21 individuals to provide context for data presented in Figure 3.2.

Predator Sightings

During our surveys, ten independent predator sightings occurred (**Table 3.5**). Predator species observed included the blue shark (*Prionace glauca*), humpback whale (*Megaptera novaeangliae*), Atlantic bluefin tuna (*Thunnus thynnus*), yellowfin tuna *(Thunnus albacares*), dolphin sp., harp seal (*Pagophilus groenlandicus*), and killer whales (*Orcinus orca*), and all observations occurred within close proximity of farm bays (≤1km). Of the ten predator sightings, all occurred within or in immediate proximity to bays containing active sea farms. All sites within the 3km radius of the sightings were active, and no sightings occurred within a 3km radius of a fallow site. In active bays, we sighted one predator for every 12.4 km surveyed, and had the encounter rate been the same for fallow bays, we would have expected 3 predator sightings. In 2016, three predator sightings occurred around farm sites in Fortune Bay (n=1) and Bay D'Espoir (n=2).

It is also important to note that although each sighting constituted one independent predator observation, there may have been more than one predator actually present. For example, we sighted bluefin (*Thunnus thynnus*) and yellowfin (*Thunnus albacares*) tuna around farm sites in Bay D'Espoir and Fortune Bay, and in each of these instances multiple individuals were present (multiple individuals were sighted breaching the surface simultaneously), but we were unable to quantify the total number of individuals directly as the maximum sighted concurrently was three.

Discussion

In our study, we combined predator sightings with hydroacoustic data to examine the effects of sea cage aquaculture on top-down ecosystem control. Top-down ecosystem control is a function of predation and the mechanisms through which consumptive and non-consumptive risk effects

affect the behavior and demographics of prey species. Sea cages have a strong attractive effect on demersal and pelagic fish species (Dempster et al. 2002; Dempster et al. 2004; Boyra et al. 2004; Tuya et al. 2006), and the aggregative effect persists around active farms over large spatial scales (Goodbrand et al. 2013). However, the majority of studies describing this effect compare active sites to similar locations with no history of aquaculture (Dempster et al. 2002, 2004, 2005, 2009; Goodbrand et al. 2013), whereas comparatively few have utilized areas with a history of aquaculture as points of comparison to active farm locations (but see Tuya et al. 2006). Comparisons made in our study were between active sites currently producing salmon with fallow sites (all having recent history of active farming operations), which allowed us to assess the effect of ongoing productivity cycles and determine if the aggregative effect persists at these sites through active and fallow periods after the initial onset of farm activity, and as well if the strength of antipredator behavior varied with time spent within the current activity status (active or fallow).

Our results show that large pelagic predators are attracted to active sea cage aquaculture sites. Our eight predator sightings included seven different species of marine mammals and fish, and all were sighted in the vicinity of active cage sites, suggesting that bays containing active sea farm sites have higher endemic risk levels for schooling fish than fallow counterparts. Despite predator preference for active sites, we found no difference in the size (biomass) and detection rates of fish schools between the two site types. This result is interesting with respect to results of Goodbrand et al. (2013) who found that in Fortune Bay, active aquaculture operations attracted more fish biomass than similar bays with no history of aquaculture. We compared bays with active farm sites to control locations with a recent history of aquaculture (within 3 years) and found no difference in detection rates of schools between site types, and it is therefore likely that

the effect of aquaculture activities likely spans beyond periods of farm activity. Although this may be interpreted as salmon farms having no effect on the detection rates of schools, the evidence seemingly points to the contrary, with numerous studies referenced within the text of this paper have documented an aggregative effect associated with farm activity (e.g. Boyra et al. 2004; Dempster et al. 2009). This result is also interesting in the context of predator sighting data. The lack of difference in school size and detection rates between site types, coupled with the predator preference for active sites, would suggest an analogue to the leapfrog effect (Sih 1998), where predators are utilizing cues associated with their prey's food resources as a way to locate their own prey.

Although we found no differences in size or detection rates of fish schools, we did find differences in school structure, suggestive of better predator detection capabilities for schools at active sites. Increases in vertical stratification accompanying lengthening periods of active farming are likely an indicator of high likelihood of encountering predators given the importance of school structure as an antipredator mechanism. Ioannou et al. (2011) showed that larger group sizes may reduce encounter rates with predators, but the lack of difference in school size we found between control and treatment sites suggests that local school properties may be more important tools in managing predation risk than group size in predictable environments where predators know where and when they can find food. Differences in local school properties suggests variation in risk perception by schooling fish, akin to the landscape of fear (Gaynor et al. 2019), where variation in prey behavior across larger spatial environments may provide insights into the behavior of larger, more elusive predators (Ale & Brown 2009).

Sea cages provide predictable resources for wild fish, and we showed that the behavior of large apex predators is also influenced by farm activity. Despite similar detection rates of schools

between active and fallow sites, predator sightings disproportionately favored active farm sites. This result follows a large body of literature suggesting that in systems where food resources are patchily distributed, predators will aggregate in areas where their prey's food resources are most abundant (Hugie & Dill 1994; Sih 1998; Alonso 2002), a phenomenon termed the 'leapfrog effect' by Sih (1998). However, contemporary aquaculture facilities attempt to minimize food loss using underwater cameras to determine when fish cede from feeding (Ang & Petrell 1997; Zhou et al. 2018), and the potential therefore exists that mechanisms driving the attractive effect of farm activity extend beyond the availability of this food resource. Large predators do not benefit directly from excess feed (i.e. they do not directly consume food pellets), and attraction to aquaculture operations may be the result of environmental cues from farm activities (e.g. feeding barges). Our data, however, provides only shapshots of these ecosystems, and models predicting predator aggregation around prey food resources are contingent on dynamic movement by both predator and prey between resource patches (Hugie & Dill 1994; Sih 1998). Limiting excess feed via industry practice may necessitate dynamic foraging behavior for schooling fish found around farm sites, as large aggregations may not sustain off pellet feed alone. Benoit-Bird & MacManus (2014) showed that data with temporal dimensions pertinent to individual organisms can be used to describe patterns in pelagic ecosystem function, and examining the behavior of predators and schooling fish at temporal scales relevant to environmental cues attracting predators and prey to aquaculture sites may supplement our understanding of spatial dynamics (predator/prey movement) in these systems.

In undisturbed pelagic systems, predators utilize environmental cues to locate prey when it is most aggregated during diurnal cycles (Benoit-Bird & McManus 2014). Vertical zooplankton migrations were shown to affect the behavior of dolphins (top-predators),

suggesting that patterns in basal resource availability create an ecosystem-level effect in marine pelagic systems (Benoit-Bird & Au 2003). As a naturally occurring process, 'critical foraging periods' created by these plankton migrations spanned short temporal durations (~30 min) (Benoit-Bird & McManus 2014), and localized prey sources for predators to exploit (intermediary consumers feeding on plankton). Sea cages have provided an interesting analogue to this effect for marine predators, as farm activity attracts large quantities of small pelagic fish (Dempster et al. 2004) over relatively small spatial scales (Dempster et al. 2009; Goodbrand et al. 2013) within the context of pelagic marine ecosystems. The presence of sea farms affects saithe (*Pollachius virens*) behavior both within years where Uglem et al. (2009) showed that saithe spent 8-10h d^{-1} in the immediate vicinity of cages over a three month period, and between years where Otterå & Skilbrei (2014) showed that annual migration patterns of saithe changed due to the presence of sea farms. Comparatively longer residency times of saithe around farm sites were observed by Uglem et al. (2009) (relative to results of Benoit-Bird & McManus 2014) and suggest that farm activity creates prolonged periods where prey are comparatively more aggregated relative to other points in their circadian cycle. In our study, all predator sightings occurred on the periphery of bays containing active farm sites, and no predators were sighted in direct proximity to farm infrastructure (i.e. in the immediate vicinity of cages). Although we observed differences in school morphologies between sites differing in the temporal duration of its current activity status, our data provides only snapshots of this system and examining dynamic patterns in predator distributions over temporal scales relevant to organisms and farm operations may provide further insights into the effects of predator aggregation around active farm sites.

Given the size of pelagic ecosystems, prolonged attraction of predators to relatively small spatial areas may have effects that extend beyond directly quantifiable differences in school structure (effects of predator behavior may manifest outside of prey behavior alone). Large aggregations of mid-level consumers around sea farms are driven in part by the availability of an alternative, and highly predictable food resource (excess feed) (Sanchez-Jerez et al. 2011; Bjordal & Johnston 1993). Numerous studies have demonstrated the relative importance of food and predation risk in both laboratory and field settings, and the relative impact of each can be offset by the availability of food (Abrahams & Dill 1989) and relative safety from predators (Wirsing et al. 2007; Heithaus et al. 2005). Because aggregations of mid-trophic level consumers persist around active farms, the energetic benefits of doing so must outweigh risks posed by increased predator presence. Studies have focused on the energetic benefits of farm feed for wild fish (Dempster et al. 2011; Barrett et al. 2018), and understanding the relative impact of changing top-down forces (behavior of predators) on the structure of pelagic ecosystems occupied by fish farms requires concurrent understanding of the relative value associated with food- and safety-related benefits provided by sea farms.

Within the context of increasing industry presence in Atlantic Canada, our results show that aquaculture activities directly affect top-down processes that structure pelagic marine ecosystems by attracting large predators. However, despite the evidence we provide, it is next important to add data with appropriate temporal dimensions to describe dynamic processes in this system. Given that significant proportions of ecosystem-level activity can be compressed into very short temporal windows in undisturbed pelagic systems, it is important to determine if these systems function similarly, or if the addition of food and structure resources for wild fish create more prolonged, dynamic cycles in animal behavior caused by farm activity relative to

naturally occurring processes (Benoit-Bird & McManus 2014; Benoit-Bird & Au 2003). Sea farms provide food and safety for wild fish, and understanding the comprehensive impact of top-down forces requires that the relative value of these, as well as other potentially unacknowledged benefits, be quantified for mid-level trophic consumers frequently occurring at these sites. The persistence of aggregations around farm sites suggest that the energetic benefits of these sites outweigh the risk-associated costs, and differences in school morphologies between our site types show that increasing vertical stratification may allow fish schools to tolerate high encounter probabilities with predators.

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Figures & Tables

Table 3.1 Settings of echosounder used during surveys. Echosounder calibration occurred immediately prior to each of our surveys using the standard tungsten-carbide sphere method.

Device Settings	Echosounder
Type	Simrad EK60
Beam Characteristic	Split Beam
Frequency	38kHz
Individual Beam Angle	6.98°
Pulse Length	1.024ms
Pulse Rate	$1s^{-1}$
Transmission Power	2kW
Time Varied Gain	20LogR
Range	Variable

Table 3.2 Fallow/Active bays between years. Old Woman Cove, Little Burdock Cove, and Mal Bay were not surveyed in 2016, 2014, and [Fall] 2015, respectively, due to logistical difficulties, and Salmonier Cove, Red Cove, Murphy's Cove, and Harbor Breton were not surveyed in 2014 due to limitations in our survey plan.

	Survey			
Site Name	**Fall 2014** (Sept 17-19)	**Spring 2015** (July 28-31)	**Fall 2015** (Oct 5-9)	**Fall 2016** (Sept 19-23)
Poole's Cove	Active	Active	Active	Fallow
Hickman's Point	Active	Active	Active	Fallow
South East Bight	Active	Active	Active	Fallow
McGrath Cove	Active	Active	Active	Fallow
Old Woman Cove	Active	Active	Active	*not surveyed
Deep Water Point	Fallow	Active	Active	Active
Little Burdock Cove	*not surveyed	Active	Active	Active
Rencontre Island East	Fallow	Active	Fallow	Active
Mal Bay	Active	Active	*not surveyed	Active
Ironskull	Fallow	Fallow	Active	Active
Salmonier Cove	*not surveyed	Active	Fallow	Active
Red Cove	*not surveyed	Fallow	Fallow	Fallow
Murphy's Cove	*not surveyed	Fallow	Fallow	Active
Harbor Breton	*not surveyed	Active	Active	Active

Table 3.3 Number of transects as well as sampling effort allocated to each of our survey bays across our four surveys. Number of transects within a respective bay was determined by bay area relative to total area sampled with the minimum number of transects in any one bay being 3. Values of 'NA' indicate that the respective bay was not surveyed during that cruise. Asterisks indicate the loss of transect data due to technical difficulties with our onboard recording system.

	Number of Transects					Distance Sampled (km)			
Site Name	**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**		**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**
Poole's Cove	9	11	12	9		14.232	17.659	18.159	13.629
Hickman's Point	6	7	7	7		8.454	10.887	10.928	10.078
South East Bight	3	3	3	3		1.992	1.949	2.012	2.321
McGrath Cove	3	2*	3	3		2.94	1.44*	1.963	2.185
Old Woman Cove	6	2*	3	NA		2.42	0.539*	1.05	NA
Deep Water Point	4	3	4	3		3.851	2.486	2.557	2.632
Little Burdock Cove	NA	3	4	3		NA	1.484	1.67	0.912
Rencontre Island	3	3	3	3		2.416	1.732	1.836	1.33
Mal Bay	9	5	NA	5		7.83	4.492	NA	4.242
Ironskull	6	5	5	5		6.635	4.487	3.917	4.405
Salmonier Cove	NA	3	3	3		NA	1.915	1.51	1.997
Red Cove	NA	3	3	3		NA	1.613	1.374	1.849
Murphy's Cove	NA	7	6	4		NA	7.418	5.847	4.336
Harbor Breton	NA	15	15	17		NA	13.999	11.319	10.971

Table 3.4 Echoview school detection module settings.

Device Settings	Module Detection Settings
Minimum Detection Threshold	-70dB
Maximum Detection Threshold	0dB
Minimum Total School Length	2.0m
Minimum Total School Height	2.0m
Minimum Candidate Length	2.0m
Minimum Candidate Height	2.0m
Maximum Vertical Linking Distance	5.0m
Maximum Horizontal Linking Distance	5.0m

Table 3.5 Predator sightings over the course of four successive surveys. ‘Active’ and ‘Fallow’ columns represent the number of respective bay type within 3km of the predator sighting.

Predator	**Survey**	**Location**	**Active (#)**	**Fallow (#)**
Blue Shark	Fall 2014	Pooles Cove	4	0
Tuna (*Bluefin*)	Fall 2015	Pooles Cove	4	0
Harp Seal	Fall 2015	Ironskull	1	0
Tuna	Fall 2016	Rencontre Island	4	0
Humpback Whale	Spring 2015	Rencontre Island	4	0
Dolphins	Spring 2015	Rencontre Island	4	0
Harbor Porpoise	Spring 2015	Murphy's Cove	1	0
Humpback Whale	Spring 2015	Harbor Breton	1	0

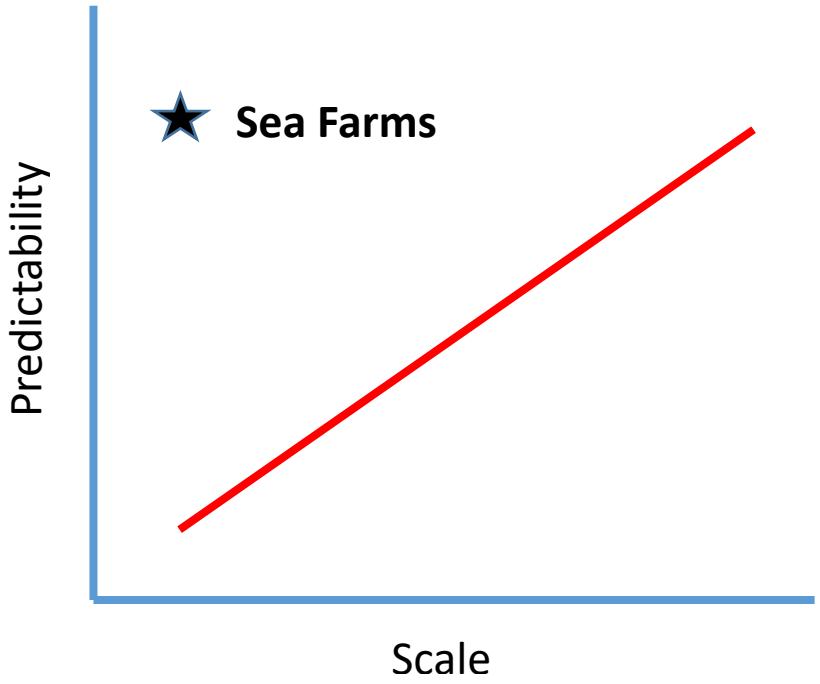

Figure 3.1. Relationship between predictability and scale. Environments become more predictable with increasing spatial and temporal scales. Anthropogenic activities in marine environments such as sea farms create microcosms of predictability that contradict the traditional ecological relationship depicted by the red line.

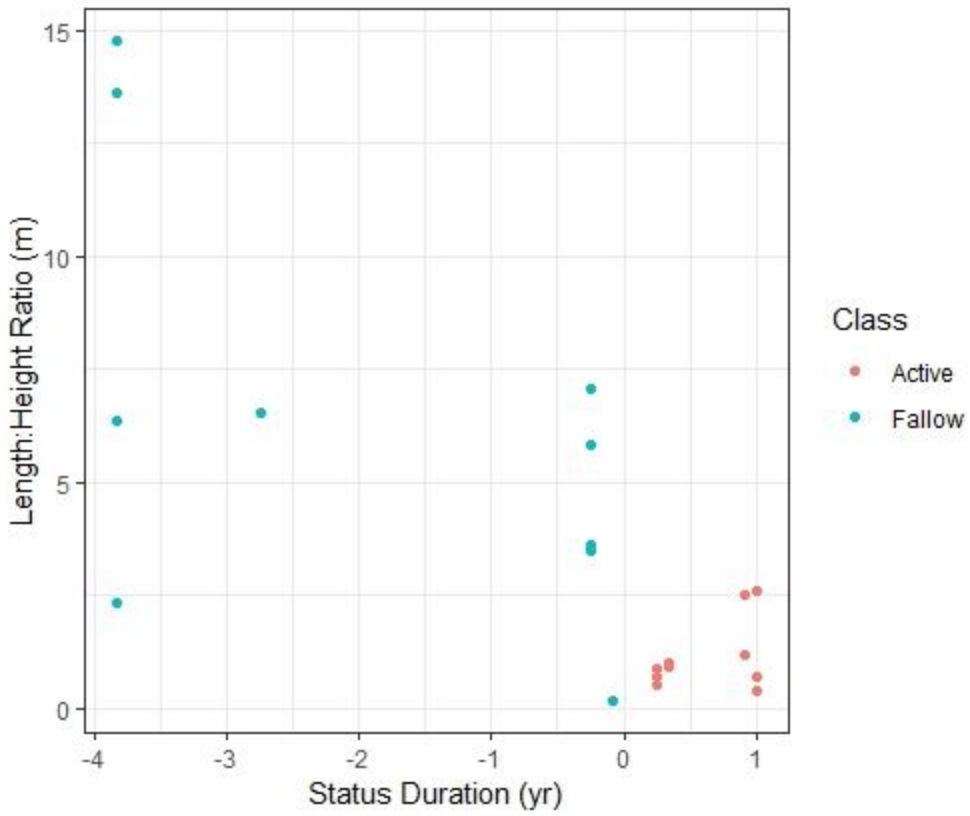

Figure 3.2. Length:Height ratio of schools (red/blue points are individual schools) with respect to activity status. Class (activity status) indicates the number of years spent in active (> 0) or fallow (< 0) states. Active bays (n=11) are indicated by red points, fallow bays (n=10) are indicated by blue points.

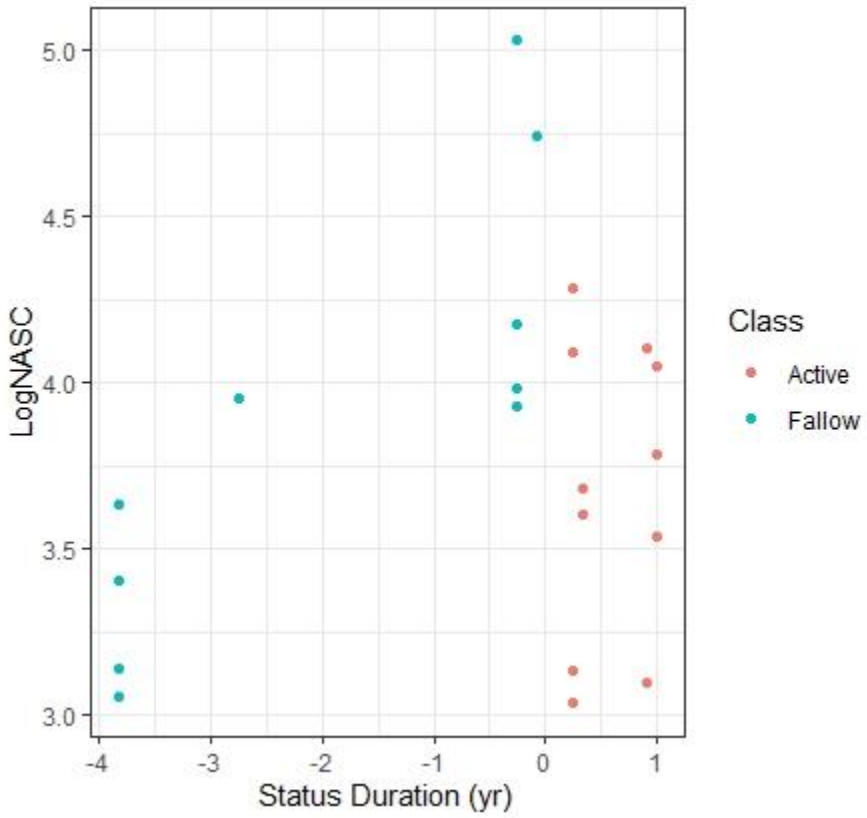

Figure 3.3 Log-transformed estimates of school (red/blue points are individual schools) biomass in active and fallow bays.. Eleven (n=11) Active bays and ten (n=10) fallow bays (n=10) were surveyed.

Chapter 4. **Quantifying potential bottom-up effects associated with marine Salmonid aquaculture**

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Abstract

Ecosystems are structured by a combination of top-down and bottom-up forces. In marine environments, spatiotemporal variation in food availability can affect the behavior of animals through the entirety of the food web, and this variation subsequently has significant effects on the structure of these ecosystems. Marine aquaculture operations attract wild fish to predictable food resource patches, and it is unclear whether this aggregative effect is generated by the availability of novel resources provided by farm sites (excess fish feed and physical structure), or due to broader environmental changes relating to aquaculture activities such as changes in regional primary productivity. We utilized hydroacoustic surveys and satellite imagery to quantify productivity trends, and used these data to describe bottom-up effects affecting the distribution of marine organisms associated with marine aquaculture across multiple spatial scales. Our results suggest that the effects of aquaculture operations on marine environments are not evident in productivity trends at large spatial scales, while at smaller scales systems containing aquaculture operations are adapting to aquaculture-related environmental changes relative to previous surveys conducted on the same systems with respect to the distribution of intermediary consumers and basal resources.

Introduction

Marine ecosystems are structured by a combination of top-down and bottom-up forces (Verity & Smetacek 1996). Top-down forces are largely the result of predation (and the various subcomponents of predation risk; see Lima 1990 and Gaynor et al. 2019) and associated processes regulating the demographics of lower-level consumer species, while bottom-up forces are driven by primary productivity and associated processes affecting the upward flow of energy through food webs. Herbivores (or primary consumers) are an important link between primary producers and upper levels of food webs because of their role in converting plant biomass into energy that may then transfer to higher-order consumer species. Environmental conditions are also important in determining the strength of bottom-up effects (see Walther 2010), as they can strongly influence the demographics of primary producers with subsequent effects on the larger food-web structure (Wollrab et al. 2012). Understanding factors that affect system-wide productivity and subsequently the demographics of herbivorous species is therefore an important link in our understanding of how ecosystems are regulated by the flow of energy from primary producers to higher-order consumer species (bottom-up effects).

For all animals, capture and consumption of enough food resources to meet energetic demands is essential for survival, and the resulting foraging decisions made by these animals significantly affect community structure (Brown et al. 2001; Kotler et al. 1994). Modeling approaches have largely considered foraging a stochastic process, where animals make foraging decisions based on long-term estimates of prey encounter rates (Stephens & Krebs 1986). The distribution of food resources across different habitats has also been used as a baseline to determine the impact of various ecological forces on animal behavior by measuring departures from fitness-maximizing spatial distributions (Fretwell & Lucas 1970). However, bottom-up

forces affect community structure simultaneously alongside top-down forces and animals determine habitat quality by weighing predation risk against potential foraging gains (Werner et al. 1984), and because of the interactive nature of these two ecosystem forces understanding the relative impact of each on animal behavior is difficult.

Bottom-up ecosystem processes have been quantified mostly within the context of classical foraging theory—animals make foraging decisions with some preconceived notion of prey encounter rates and can instantaneously adjust their distributions to changes in prey distributions (Stephens & Krebs 1986). In marine environments, changes in animal distributions in response to food resource availability and predation risk may be significantly more dynamic than described by these classical foraging models (Benoit-Bird & MacManus 2014; Benoit-Bird & Lawson 2003), and may result from predators' ability to track fine scale changes in prey abundance in highly variable environments (Suraci & Dill 2012) as well as plasticity in behavioral responses (of prey) to predators with variable feeding capacities (Nøttestad et al. 1996; Nøttestad & Axelsen 1999; Nøttestad et al. 2002). However, recent research in marine ecosystems suggest that bottom-up processes have significant bearing on risk perception in intermediary trophic species (Trussell et al. 2006; Trussell et al. 2008), and as such the effects bottom-up processes on ecosystem structure may be more pronounced in the ocean relative to terrestrial and freshwater counterparts (Preisser et al. 2005).

In marine pelagic systems, bottom-up processes can cause significant changes in the spatial distribution of animals over short temporal windows in response to environmental cues indicating food availability. Benoit-Bird & McManus (2014) showed that diel zooplankton migrations initiated periods of intense foraging activity across very short (<1hr) temporal windows that extended up to top predators where dolphins (*Stenella longirostris*) adopted

specific foraging behaviors in response to foraging behavior of their prey (smaller fish foraging on plankton). For smaller pelagic fish vulnerable to dolphin predation, foraging on plankton prey reflects their perception of predation risk relative to potential energetic gains during these periods, where the benefits of abundant plankton prey outweighed the potential cost of increased predator abundance. For these fish, habitat quality is determined by assessing both predation risk and resource availability (see Werner et al. 1984), and the relative structural homogeneity of marine pelagic habitats limits use of the physical environment to control risk as is possible in more structurally complex marine habitats (Heithaus et al. 2005; Wirsing et al. 2007). However, human activities alter marine pelagic ecosystems (by introducing spatiotemporally predictable resources for wild animals) through practices such as aquaculture (Dempster et al. 2002; Dempster et al. 2004; Dempster et al. 2009) and offshore oil infrastructure (Todd et al. 2019) that can have significant effects on both physiology (Barett et al. 2018; Dempster et al. 2011) and/or distribution of animals across larger spatial environments (Uglem et al. 2014; Goodbrand et al. 2013; Uglem 2009). Where pelagic animals are typically relatively dispersed across the larger areas outside of critical foraging periods, supplementing pelagic ecosystems with novel resources (food, structure) attracts significant amounts of wild animals spanning a large trophic breadth (Pajuelo et al. 2016; Cremer et al. 2009; Dempster et al. 2009; Tuya et al. 2006; Boyra et al. 2004; Dempster et al. 2004), but the mechanisms that allow these aggregations to persist are still unclear. In the case of aquaculture, active farming operations attract predators (Dempster et al. 2018) and it is therefore likely that the risk environment around these sites is high compared to similar locations without active farms. However, the persistence of fish aggregations despite elevated predator abundance suggests that the effect magnitude of bottom-up processes is comparative to the effect magnitude of top-down processes in these habitats, and as well several

studies suggest that the persistence of aggregations around farm sites is partially driven by increased productivity around active farms (Machias et al. 2005; Giannoulaki et al. 2005; Machias et al. 2006).

In marine environments, habitat-specific landscape features are important determinants of risk perception, and may allow animals to forage in highly productive areas despite higher encounter rates with predators (Heithaus & Dill 2006; Wirsing et al. 2007). Sea cage aquaculture sites provide food in the form of excess fish feed that falls through cages uneaten (Dempster et al. 2004; Boyra et al. 2005; Dempster et al. 2009), as well as physical structure (farm infrastructure) that also may benefit certain species (Tuya et al. 2006). These resources are available at predictable times and locations, and may function similarly to natural landscape features that allow animals to forage in high-risk/high-reward environments without subsequent increases in mortality rates. Goodbrand et al. (2013) also used number of active cages as a proxy measure for food availability and found no difference in fish biomass around farm sites relative to the number of active cages, suggesting that excess feed is not the sole proprietor of the aggregative effect. The persistence of aggregations around farms therefore mandates that an alternative food source(s) must be available to meet the foraging demands of these fish, and increased primary productivity due to aquaculture activities may provide an explanation for the maintenance of wild fish aggregations around aquaculture sites when these aggregations are unable to sustain off pellet feed alone.

Aquaculture farms have strong impacts on benthic communities (Tomasetti et al. 2016; Holmer et al. 2010), mainly through sedimentation of the sea bottom with excess feed and fish feces from cages. However, the effects of organic enrichment on plankton communities in the upper layers of the water are not well known (but see Fernandez-Gonzalez et al. 2014), and

understanding how aquaculture activities affect productivity levels in marine environments will help to determine the relative magnitude aquaculture-related changes to marine pelagic ecosystem structure, as well as provide a mechanistic understanding of factors allowing for the persistence of large fish aggregations around active farm sites. Studies have shown that 70-80% of nitrogen lost from salmonid farms enters the surrounding environment in dissolved form at approximately 100 kgN / tonne of fish (Hall et al. 1992), providing conditions necessary for increases in local productivity. In New Brunswick, Canada, farms affect nutrient flux rates, where bays containing farms also contain comparatively larger amounts of nitrogen and carbon due to waste buildup and distribution from farms (Strain & Hargrave 2005), although no changes to regional productivity were reported. Because food plays an important role in dictating the spatial distribution of foragers in pelagic marine systems (Benoit-Bird & McManus 2014), the goal of this study is to quantify regional productivity trends, and compare these data to the relative abundance of both zooplankton and fish biomass between active and fallow farm bays to determine if the distribution of food items at small spatial scales (between aquaculture sites) matches primary productivity trends across the larger spatial landscape. We predict that regionally, major oceanographic bays containing farm operations will have higher productivity levels than those not containing aquaculture sites. At smaller scales, we predict that although productivity may be higher around farm sites, the brevity of fallow periods between productivity cycles will mask any effects of increased primary productivity due to farm activity.

Methods

System-wide trends in primary productivity

We measured primary productivity ($mgC \cdot m^{-2} \cdot day^{-1}$) using ERDDAP (Environmental Research Division Data Access Program) satellite imagery from the National Oceanic and Atmospheric Administration (NOAA) (Simons 2019) to assess annual productivity trends in Fortune Bay, Bay D'Espoir, and Placentia Bay (**Figure 4.1**). Fortune Bay and Bay d'Espoir have a recent history of extensive aquaculture pressure, while Placentia Bay has only recently been approved for salmonid production and has no recent history of active farming, and we compared primary productivity data among these three locations from 2014 to 2017. Primary productivity values were calculated from individual grid cells within each satellite image, and each grid cell covered $4km^2$ and constitutes a monthly average for the respective cell. Only cells within each bay were used in our analysis and for all years (2014—2017), months Jan—Feb—Mar were excluded as cloud and ice cover obstructs satellite visibility in the area during these months. To determine annual productivity values, monthly averages from each grid cell were averaged for each year. These values were then compared across years and between bays, and these data were also compared to our hydroacoustic survey data to determine if regional productivity trends matched trends in zooplankton and fish abundance in Fortune Bay. In total 151 grid cells (604 km^2) per image were analyzed in Placentia bay, 25 (100 km^2) in Bay d'Espoir, and 30 (120km^2) in Fortune Bay.

Hydroacoustic Surveys

We used hydroacoustic surveys to investigate differences in zooplankton and fish abundance between active and fallow farm sites in Fortune Bay. We used measurements of total area

backscatter (NASC; see MacLennan 2002) to test for differences in the abundance of both plankton and wild fish between active and fallow aquaculture sites, and these data were used to investigate the effects of food availability on the spatial distribution of mid-level consumer fish species comprising farm aggregations, and as well to determine the relative contribution of food availability to the cumulative aggregative effect generated by farm activity.

Hydroacoustic surveys were conducted aboard a 10m dedicated hydroacoustic research vessel the RV Gecho II. Data were obtained using a Simrad EK60 38/120kHz split-beam transducer **(Table 4.1).** Our echosounder was calibrated prior to each survey using a standard tungsten-carbide sphere (Simmonds & MacLennan 2008). Transducers were mounted off the port beam on a winch system, allowing for easy deployment and retrieval. Data were recorded directly on ship-board computer systems that also provided live viewing capabilities. Although plankton signals are generally stronger on 120kHz echosounders, repeated technical difficulties that we were unable to remedy made these data unusable, and we therefore obtained zooplankton biomass estimates from our 38kHz sounder. Use of our 120kHz sounder would have provided higher resolution data from the upper layers of the water column as higher frequency sounders suffer at increased range (particularly in salt water) (Simmonds & Maclennan 2008), and this would have allowed us to quantify more comprehensively the relative abundance of zooplankton taxa in the upper water column. However, krill constitute a major proportion of zooplankton biomass in Fortune Bay (Richard & Haedrich 1991) and exhibit strong diel patterns with preference for deeper habitats during daytime hours which may have afforded us some benefit using our 38kHz sounder as all of our surveys took place during daytime.

Four hydroacoustic surveys were performed between September 2014 and October 2016 at Atlantic salmon (*salmo* salar) aquaculture sites on the south coast of Newfoundland from

Harbour Breton (47°28’23” N, 55°50’06” W) through Fortune Bay (47°35’49” N, 55°24’32” W). A total of 14 different bays containing active or fallow Atlantic salmon aquaculture sites were surveyed (**Table 4.2**). Active sites contained between 8 and 24 circular net-pens, each 10m diameter and approximately 20m deep. Active cages contained salmon ranging from post-smolt to adult, and different age classes were segregated between bays. Our surveys took place over a three year period, and 9 of 14 bays were surveyed during active and fallow periods (between surveys) due to the timing of fish stocking/harvesting. In 2011, Goodbrand et al. (2013) surveyed the same area, but was able to utilize licensed but unused bays as control sites. Since, aquaculture operations have occurred in all of these bays, and our surveys were therefore describing bays with varying levels of aquaculture-related impacts with respect to production cycles (active/fallow periods) within individual bays. Although the initial plan called for equivalent survey replicates in spring and fall months so that seasonal comparisons could be made, we were constrained significantly by logistical difficulties that resulted in the completion of one spring survey and three fall surveys (sampling dates reported in **Table 4.2**), and although seasonal differences likely exist, this was controlled for in the context of our analysis by including active and fallow bay data from all surveys.

We used a randomized transect method to survey each bay, and sampling effort devoted to each bay was based on bay area relative to total area sampled (**Table 4.3**). Goodbrand et al. (2013) showed that the aggregative effect of sea farms on fish in this location occurred at the bay level, and we were therefore able to allocate our survey efforts to the entire bay rather than only the immediate vicinity of the net pens, and individual bays were treated as independent observations. Transects were run parallel to the bay entrance at 5-7kt, and locations within each bay were randomly selected from the total number of non-overlapping transects possible (as a

function of bay area and acoustic beam width). For smaller bays, the minimum number of transects performed was 3.

Echoview software (version 7.0.97) was used to process our data. All non-biological backscatter (i.e. farm infrastructure), as well as a 3m zone extending downward from the transducer face (4m total depth from surface) was excluded from our analysis. To determine plankton NASC estimates, we isolated known backscatter signal ranges for krill species (see Simmonds & MacLennan 2002), as Arctic (*Thysanoessa raschii*) and Northern krill (*Meganyctiphanes norvegica*) account for over 67% of zooplankton biomass in both Bay d'Espoir and Fortune Bay (Richard & Haedrich 1991). Backscatter estimates are therefore assumed to reflect the abundance of major [naturally-occurring] prey items for intermediary consumer species that aggregate around farm sites in the region (Goodbrand et al. 2013). For our zooplankton analysis, we excluded biological signals at thresholds greater than -70dB, as ensonified targets below this echo threshold are likely fish, and acoustic target strength of krill ranges from -70dB to -100 dB (Stanton & Chu 2000) at 38kHz. NASC estimates for fish were generated by integrating transect backscatter data at a threshold of -70dB. To assess the impact of food availability on the distribution of fish, we divided log-transformed NASC values for fish by values for plankton, and these ratio quantities therefore reflected the relative abundance of fish to plankton within the respective bay.

$$\text{Biomass}_{\text{Fish/Plankton}} = \text{logNASC}_{\text{Fish}} / \text{logNASC}_{\text{Plankton}} \quad [1]$$

Results

System-wide trends in primary productivity

We examined trends in regional productivity between Fortune Bay, Bay D'Espoir, and Placentia Bay (**Figure 4.1**) to determine if primary productivity trends were similar to zooplankton trends observed at smaller spatial scales from our hydroacoustic surveys within Fortune Bay. We found significant differences between years ($F_{3,7610} = 151.4$, $p < 2.2 \times 10^{-16}$), locations ($F_{2,7610} = 26.1$, $p = 5.16 \times 10^{-12}$), and as well an interactive effect between year and location (($F_{6,7610} = 5.61$, $p = 8.0 \times 10^{-6}$) showing differences in productivity values between locations in different years (**Figure 4.2**). Average annual productivity values were also highest in Fortune Bay and lowest in Placentia Bay, with Bay d'Espoir lying intermediate. We also performed a post-hoc tukey test, and found significant inter-annual differences between all years except 2015—2014 ($p < 0.00001$ for all yearly comparisons except 2015-2014). We also chose to incorporate data from 2017, despite not having comparable hydroacoustic data from 2017, as this provided context for the sharp bump in regional productivity across all bays observed from 2015-2016.

Hydroacoustic Surveys

We treated bays containing farm sites as statistically independent samples based on results from Goodbrand et al. (2013), and sampled a total of 99.1 and 34.4 nautical miles from active and fallow sites (n=35, n=13 respectively). Plankton backscatter estimates taken from our 38kHz echosounder data were based on krill signal profiles at this frequency (Stanton & Chu 2000), and our 120kHz echosounder was unused due to repeated technical difficulties, resulting in our inability to directly quantify a minority subset of zooplankton species found in Fortune Bay/Bay d'Espoir with signal profiles outside the range of krill backscatter. We found no difference in

mean NASC values from fish ($F_{1,42}$ = 0.2044, p = 0.6535) and plankton biomass ($F_{1,42}$ = 0.0652, p = 0.7997) (**Figure 4.3**) between control and treatment sites, and as well no difference across years ($F_{2,42}$ = 0.5765, p = 0.5663 ; $F_{2,42}$ = 2.81, p = 0.7141).

We also calculated the comparative abundance of fish to plankton biomass within individual survey bays to determine the spatial relationship between fish and zooplankton prey by dividing log-transformed values of fish and plankton biomass (**Eq. 1**). We found that the comparative abundance of fish to plankton did not differ between fallow and active sites ($F_{1,42}$ = 0.2618, p = 0.6116) and across years ($F_{2,42}$ = 0.1091, p = 0.8969) (**Figure 4.4**).

Discussion

We examined primary productivity trends between three major bays on Newfoundland's south coast, and compared these data to the comparative abundance of fish to zooplankton between active and fallow farm sites in Fortune Bay and the surrounding area. We compared system-wide trends in primary productivity to measure ecosystem level responses to aquaculture activity. Cumulatively, our results suggest that significant differences in productivity values observed between years are not reflected at smaller spatial scales based on the lack of statistical differences observed between the comparative abundance of fish to plankton between active and fallow farm bays, although these data are trending towards increases in comparative biomass. As well, our results suggest that ecosystem-level responses to aquaculture activities have changed relative to results from Goodbrand et al. (2013) who found more fish in bays containing active farms relative unused ones. Our study differed in that we were able to compare active and fallow farm sites all with recent (<3yr) history of aquaculture, which gave us the ability to examine long-term ecosystem responses to changing environmental conditions with respect to the same system surveyed in 2011 by Goodbrand et al. (2013). Similar long-term responses to aquaculture

have been documented in the eastern Atlantic as well, where Otterå & Skilbrei (2014) found changes in residency behavior of saithe (*Pollachius virens*) in coastal environments due to the presence of salmonid farm sites. Lack of difference in fish biomass between active and fallow sites observed in our study would suggest that the effects of aquaculture within smaller bays in southern Newfoundland persist beyond periods where farm sites are actively producing fish. Cumulatively, our results here indicate that aquaculture operations impact marine environments beyond periods of farm activity, and that the ecological footprint created by these sites after the initial onset of active farming remains through fallow periods.

Although our data shows increases in system-wide productivity, these effects must be considered in the context of the structure of local ecosystems. Because active farms also attract predators (see Uglem et al. 2014), the benefits of increased food resource abundance (plankton, excess feed) at active sites relative to fallow ones may be offset by increased predation risk with respect to perceived habitat quality. Our hydroacoustic data suggests equal food availability between control and treatment sites for intermediary consumers, but with drastic differences in predation risk with fallow sites having low risk (low predator abundance) and moderate food availability, and active sites having high risk (high predator abundance) and moderate food availability. In the context of our analysis of fish distribution, this would suggest that spatial distributions (which are the result of habitat quality assessment by fish) are dictated by food resources rather than predation risk, meaning that the potential energetic benefits associated with farm sites outweigh the perceived risk associated with occupying these habitats (see Gaynor et al. 2019). However, it is likely that additional benefits are provided by farm sites, whether from benthic enrichment (Tomasetti et al. 2016), excess feed (Bjordal & Skar 1993; Dempster et al. 2011; Barrett et al. 2018), or otherwise, due to the persistence of fish aggregations at active farm

sites despite increased predation risk. Studies have documented significant consumption of farm feed and changes in body condition in farm-associated wild fish (Barrett et al. 2018; Dempster et al. 2011), and quantifying the amount of excess feed consumed by farm-associated fish in Newfoundland may provide further insights to the cumulative effects of food resources on the distribution of foragers across the larger spatial environment. Benoit-Bird & McManus (2014) showed that bottom-up processes initiate periods of intense foraging activity during critical temporal windows (<1hr) for pelagic consumers ranging from zooplankton to large predators, and dolphins more than doubled feeding activity during these periods of plankton activity. Given the breadth of effect that basal resources have on marine food webs, these critical periods likely constitute a large component of pelagic ecosystem structure. Understanding how aquaculture feeding operations influence these critical foraging periods in pelagic ecosystems is therefore needed to further quantify the effects on bottom-up ecosystem processes.

As well, it may also be important to investigate seasonal effects on these critical foraging periods. The coastal waters of Newfoundland are characterized by seasonal predator regimes, with, for example, migrating whales being largely present in the spring, and absent through the rest of the summer/fall months. Although our initial survey plan was also designed to test seasonal differences (spring/fall) in productivity around active and fallow farm sites, logistical setbacks resulted in only one survey being performed in the late spring, and we were thus unable to make seasonal comparisons. This does, however, merit further investigation, as the diversity of animals present in coastal waters changes from spring to fall, which likely affects the way individuals perceive and respond to predation threats (e.g. Nøttestad & Axelsen 1999; Nøttestad et al. 2002) and may have direct effects on the behavior of animals during these critical foraging periods.

Although excess feed is the most often-cited driver of fish aggregations around aquaculture sites (Bjorn & Skar 1993; Dempster et al. 2011; Barrett et al. 2018), changes to the physical environment caused by farm infrastructure may also play an important role in attracting and maintaining aggregations of wild fish. Tuya et al. (2006) found a 50-fold decrease in the aggregative effect generated by active farm sites after the cessation of farming in the Gran Canary Islands, suggesting that the aggregative effect may be driven partially by physical farm infrastructure for a minority contingent of aggregated species. Lower endemic productivity levels in warm water regions like the Grand Canary Islands may inflate bottom-up effects created by introducing artificial food resources around farm sites and subsequently creating comparatively larger disparities in food availability between habitat patches, where results from our plankton analysis indicate that the magnitude of bottom-up effects in temperate systems may be offset by naturally higher levels of primary productivity. However, where excess feed may provide additional food resources that we were unable to account for in our study and this increase accompanied by high risk levels due to the attraction of predators to farm activity, farm infrastructure likely provides additional benefits for fish in the form of a refuge from elevated risk of encountering predators, potentially similar to natural landscape features that allow animals to tolerate increased exposure to predation risk (Heithaus et al. 2006; Wirsing et al. 2007).

Our hydroacoustic data have provided insights into the aggregative effect on fish generated by sea farms, but these data also show long-term environmental responses to predation risk with respect to results from Goodbrand et al. 2013) whose surveys took place 3 years prior to our initial survey in 2014. Comparison of active sites to fallow sites with recent history of active productivity allowed us to show that the effects of aquaculture operations persist outside

of active farming periods at farm sites. Goodbrand et al. (2013) showed that active farm sites attract animals to active farm sites (rather than unused bays) at comparatively larger spatial scales than previously documented (e.g. Dempster et al. 2009), and our data suggests that the aggregative effect may not be limited to bays containing active farms. We found no difference in the comparative biomass of fish and zooplankton between the two. Trends from our zooplankton and fish data did not match increasing regional primary productivity across years, where we saw a small increase in fish and plankton biomass from 2015-2016. However, fish and plankton abundance was higher in control than treatment bays in 2016, which may have been because two major bays containing significant farm activity (Poole's Cove and Hickman's Point, **Table 4.1**) had recently been harvested (within 3 months) and likely still bore some effects of active farming with respect to behavioral responses and abundance of wild organisms to these sites at that time. However, this requires further investigation, as the relative time duration spent within the current activity status can affect the impact magnitude these sites have on the behavior of wild organisms (Chapter 3, this thesis) and subsequently pelagic ecosystem structure, and our data lacked the fine-scale temporal resolution necessary to investigate such effects over short time periods (days-months). As well, the importance of marrying spatial data such as ours with temporal data at relevant scales (Benoit-Bird & McManus 2014) will provide a more comprehensive understanding of processes that structure ecosystems.

Our results may also be affected by industry attempts to limit the amount of excess feed from cage feedings that becomes available to wild fish as lost feed constitutes economic loss for industry practitioners. Although it is clear that this food source still constitutes a portion of farm-associated fish diets, increasing efficacy at limiting the amount of available feed for wild fish will likely affect the distribution of these fish species between farm sites (see Otterå & Skilbrei

2014; Uglem et al. 2014; Uglem et al. 2009) and across larger spatial environments. Direct quantification of excess feed availability is therefore an important avenue for future research, as consumption of farm feed may have long term effects on reproductive fitness in farm-associated fish species (Barrett et al. 2018; Dempster et al. 2011). We previously proposed that the effects of increasing system-wide productivity may be buffered in regions containing aquaculture operations, as these locations attract intermediary consumers compared to similar locations with no aquaculture. This would suggest that fish biomass in Fortune Bay and Bay d'Espoir is likely higher than the adjacent Placentia Bay if examined from a system-wide perspective, which would require higher food-availability in aquaculture production areas to maintain high levels of fish biomass density. As such, further investigation of bottom-up effects of aquaculture activities should focus on quantifying excess feed availability, as this will provide direct evidence of factors underlying fish aggregations around farm sites, as well as help to determine the relative value of food and structure for pelagic fish species in areas containing marine aquaculture activities.

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Figures & Tables

Table 4.1 Settings of echosounder used during surveys. Echosounder calibration occurred immediately prior to each of our surveys using the standard tungsten-carbide sphere method.

Device Settings	Echosounder
Type	Simrad EK60
Beam Characteristic	Split Beam
Frequency	38kHz
Individual Beam Angle	6.98°
Pulse Length	1.024ms
Pulse Rate	$1s^{-1}$
Transmission Power	2kW
Time Varied Gain	20LogR
Range	Variable

Table 4.2 Active/fallow bays between years. Old Woman Cove, Little Burdock Cove, and Mal Bay were not surveyed in 2016, 2014, and [Fall] 2015, respectively, due to logistical difficulties, and Salmonier Cove, Red Cove, Murphy's Cove, and Harbor Breton were not surveyed in 2014 due to limitations in our survey plan.

	Survey			
Site Name	**Fall 2014** (Sept 17-19)	**Spring 2015** (July 28-31)	**Fall 2015** (Oct 5-9)	**Fall 2016** (Sept 19-23)
Poole's Cove	Active	Active	Active	Fallow
Hickman's Point	Active	Active	Active	Fallow
South East Bight	Active	Active	Active	Fallow
McGrath Cove	Active	Active	Active	Fallow
Old Woman Cove	Active	Active	Active	*not surveyed
Deep Water Point	Fallow	Active	Active	Active
Little Burdock Cove	*not surveyed	Active	Active	Active
Rencontre Island East	Fallow	Active	Fallow	Active
Mal Bay	Active	Active	*not surveyed	Active
Ironskull	Fallow	Fallow	Active	Active
Salmonier Cove	*not surveyed	Active	Fallow	Active
Red Cove	*not surveyed	Fallow	Fallow	Fallow
Murphy's Cove	*not surveyed	Fallow	Fallow	Active
Harbor Breton	*not surveyed	Active	Active	Active

Table 4.3 Number of transects as well as sampling effort allocated to each of our survey bays across our four surveys. Number of transects within a respective bay was determined by bay area relative to total area sampled with the minimum number of transects in any one bay being 3. Values of 'NA' indicate that the respective bay was not surveyed during that cruise. Asterisks indicate the loss of transect data due to technical difficulties with our onboard recording system.

	Number of Transects					Distance Sampled (km)			
Site Name	**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**		**Fall 2014**	**Spring 2015**	**Fall 2015**	**Fall 2016**
Poole's Cove	9	11	12	9		14.232	17.659	18.159	13.629
Hickman's Point	6	7	7	7		8.454	10.887	10.928	10.078
South East Bight	3	3	3	3		1.992	1.949	2.012	2.321
McGrath Cove	3	2*	3	3		2.94	1.44*	1.963	2.185
Old Woman Cove	6	2*	3	NA		2.42	0.539*	1.05	NA
Deep Water Point	4	3	4	3		3.851	2.486	2.557	2.632
Little Burdock Cove	NA	3	4	3		NA	1.484	1.67	0.912
Rencontre Island	3	3	3	3		2.416	1.732	1.836	1.33
Mal Bay	9	5	NA	5		7.83	4.492	NA	4.242
Ironskull	6	5	5	5		6.635	4.487	3.917	4.405
Salmonier Cove	NA	3	3	3		NA	1.915	1.51	1.997
Red Cove	NA	3	3	3		NA	1.613	1.374	1.849
Murphy's Cove	NA	7	6	4		NA	7.418	5.847	4.336
Harbor Breton	NA	15	15	17		NA	13.999	11.319	10.971

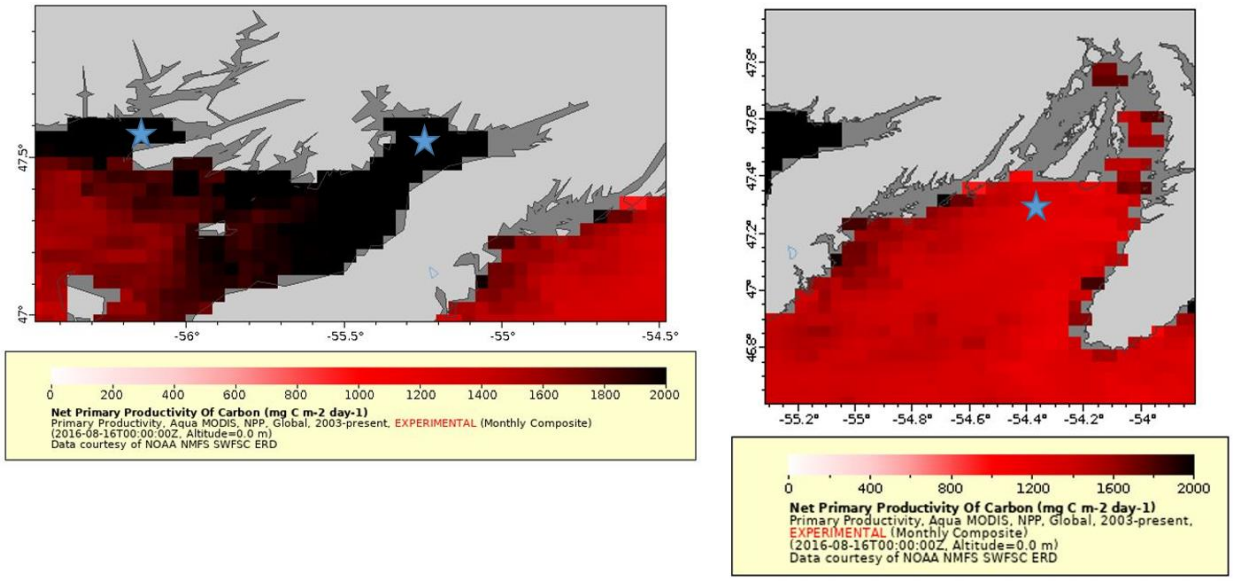

Figure 4.1 Primary productivity data from Bay d'Espoir, Fortune Bay, and Placentia Bay (blue stars) from August 2016. Left panel shows Bay d'Espoir and Fortune Bay, and the right panel shows Placentia Bay. Individual grid cells within each bay constitute approximately 4km^2. Pixels used in Placentia Bay were those above the 47th parallel, and those used in Fortune Bay and Bay d'Espoir were those above the 47.5th parallel.

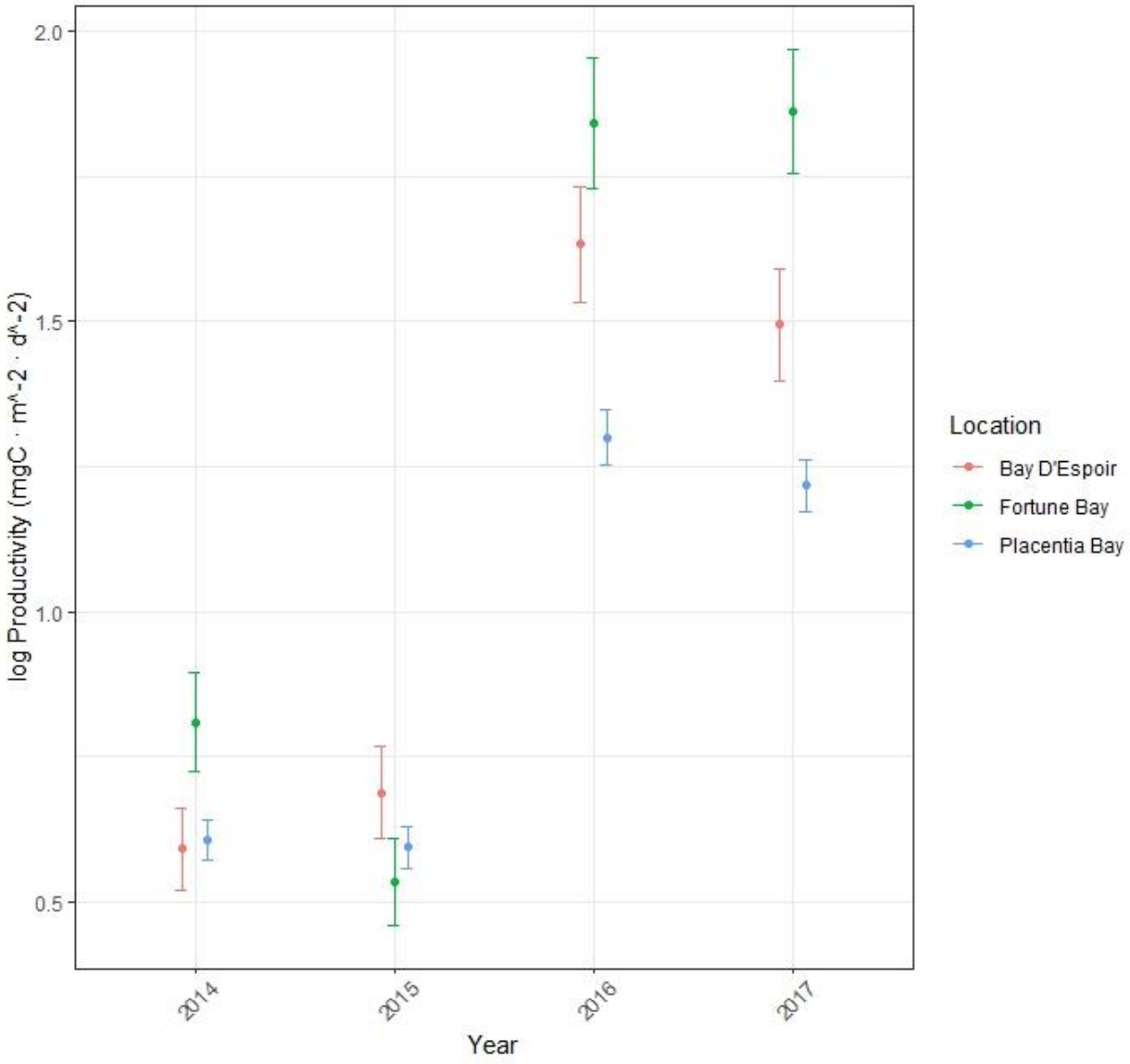

Figure 4.2 Primary Productivity trends from Fortune Bay, Bay D'Espoir, and Placentia Bay from 2014—2017. Each point constitutes the average annual productivity for each bay for months April-December. Error bars are ± one standard error from the sample mean.

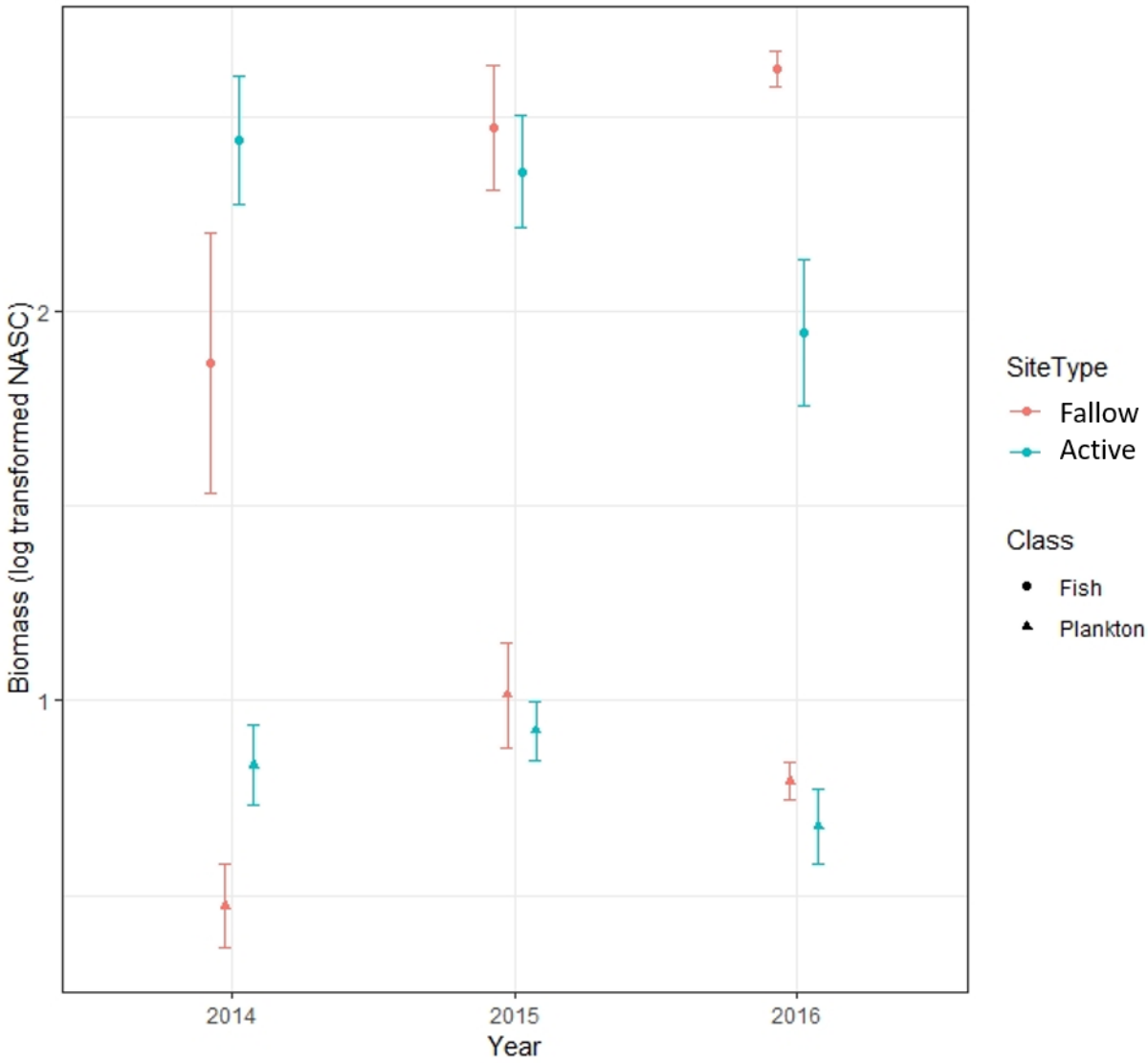

Figure 4.3 Log-transformed NASC values for fish and plankton biomass between active and fallow bays. Error bars displayed represent +/- 1 standard error from the sample mean.

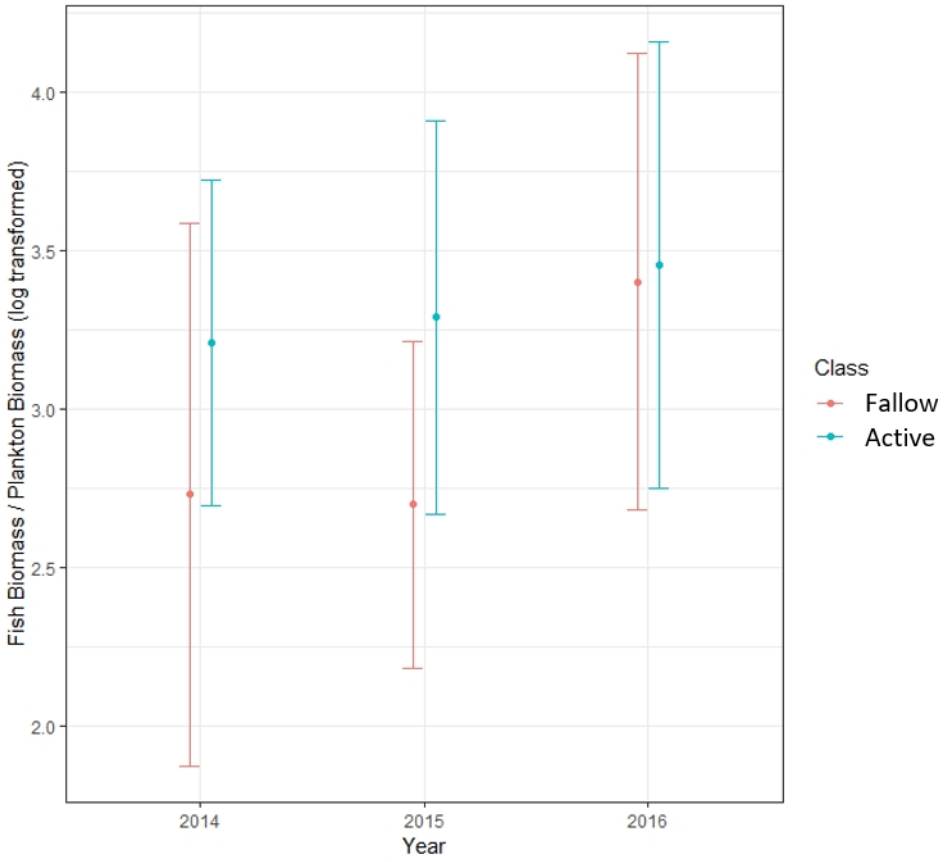

Figure 4.4 Comparative abundance of fish and plankton biomass between fallow and active sites across three years. Error bars are ± one standard error from the sample mean. Comparative biomass was calculated by dividing log($NASC_{FISH}$) / log($NASC_{PLANKTON}$), as this provided a standardized value for the relative abundance of both fish and plankton for comparison.

Chapter 5. **A comparative approach toward assessing the impacts of escaped farm-raised Atlantic salmon (*Salmo salar*) on wild conspecifics in the ocean**

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Abstract

Aquaculture operations across the globe have been steadily increasing productivity for the past three decades. Despite the impetus for aquaculture being the supplementation of worldwide fish demand without depletion of wild fish stocks, the question of whether these operations *actually* help or hurt wild fish populations in the long term still remains ambiguous. Atlantic salmon (*Salmo salar*) are farmed across the entirety of their native range, and varying degrees of genetic introgression between farm and wild stocks have been documented on both sides of the Atlantic Ocean. For farm-raised salmon that escape containment, the marine environment often constitutes the primary interaction arena with wild fish, and relative introgression risk is therefore in part dependent on marine survivorship prior to interaction with conspecifics in freshwater spawning environments. We acoustically tagged forty (n=40) wild Atlantic salmon smolts from the Conne River in southern Newfoundland and tracked their movement through an array of fixed receivers positioned at active aquaculture sites. These data were compared to acoustic telemetry data from controlled-releases of farm-raised Atlantic salmon from 2014-2016 in an adjacent fjord, and as well to a previous acoustic telemetry study examining the movement of wild Conne River smolts through aquaculture sites in Bay d'Espoir, to quantify the effect of aquaculture operations on the survivorship of both wild- and farm-raised fish in the ocean. Our results show significant differences in perception of habitat quality between wild and farm-raised salmon, where wild smolt movements were directed and they vacated coastal fjords at significantly faster rates than in previous years. Comparatively, controlled releases of farm-raised salmon in the ocean suggested repeated movements between active farm sites instead of towards fjord exit points like wild conspecifics. Cumulatively, our results suggest that significant

behavioral differences exist between wild and farm-raised Atlantic salmon, and that these differences are a likely source of mortality risk for farm fish in the ocean.

Introduction

Fish production from worldwide aquaculture operations has been steadily increasing since the 1990s (FAO 2018). Atlantic salmon (*Salmo salar*) are a staple of the European and North American aquaculture industry, and account for 4% of global fish production (FAO 2018). The impetus for aquaculture is to meet growing market demand for fish that cannot by met through sustainable exploitation of wild stocks, yet the question of whether aquaculture operations help or hurt wild fish populations in the long term remains (Naylor et al. 2000). Atlantic salmon aquaculture in Newfoundland is relatively new by world standards, and major production along Newfoundland's Coast of Bays region did not begin until the early 2000s. Comparatively, Norway has been a major producer of Atlantic salmon since the 1980s, and has subsequently had more time to gather data necessary to inform the development and effectiveness of risk-mitigation strategies aimed at limiting the dispersal of escaped farm fish in to wild environments (see Bridger et al. 2015).

Schiermeier (2003) estimated that two million Atlantic salmon escape farm containment each year within the species' native range in the north Atlantic. Farm fish effect wild stocks through genetic introgression (Keyser et al. 2018; Bolstad et al. 2017), disease transfer from farms to wild environments (Madhun et al. 2017; Madhun et al. 2015; Costello 2009), and competitive interactions that ultimately reduce lifetime reproductive output of native fish (Fleming et al. 2000). Escaped farm-raised Atlantic salmon first enter wild environments from marine farm operations, and along Newfoundland's Coast of Bays region where farms occur in close proximity to natal salmon rivers and coinciding migration corridors of wild salmon (see Hamoutene et al. 2018; Dempson et al. 2011), gaining a deeper understanding of post escape behavior will help to assess risks posed to wild salmon in marine environments. Wild salmon

populations in this area have declined in recent decades (DFO 2017). Keyser et al. (2018) showed positive correlation between farming intensity and both the number of farm-origin fish captured at local river counting fences and the magnitude of genetic impact on wild salmon stocks along the Coast of Bays suggesting the magnitude of farm activity can be used to predict the relative introgression risk posed by aquaculture operations. Morris et al. (2008) also showed that farm salmon are present in rivers nearly everywhere farm sites are present in the western Atlantic, and in some instances the number of escaped salmon exceeded (almost doubled) the total number of wild salmon adults returning to spawn in rivers adjacent to farm sites (see also Hansen & Youngson 2010). It is therefore likely that the effects of aquaculture are most pronounced within small spatial ranges of sea cages (i.e. rivers closest to farm sites may be at higher introgression risk than ones farther away), and relative introgression risk results from escape magnitude (# of individuals) and the size of local salmon populations.

For farm fish, marine survival is a major contingency of interbreeding success, and only recently have controlled release experiments been performed with ranched salmon in Newfoundland to investigate the marine behavior of these fish (Hamoutene et al. 2018). Understanding how these fish interact with local environmental conditions will inform on factors affecting marine survivorship, and ultimately help to assess relative levels of introgression risk that can be tolerated with minimal impact on local salmon populations. Studies from the eastern Atlantic have shown that release timing (Skilbrei 2010a), life stage (Skilbrei 2010a; Skilbrei 2010b), and farm density (number farms per unit area) (Fiske et al 2006) all have significant influence on post-release behavior of farm salmon. Hamoutene et al. (2018) showed similar trends from controlled releases of Atlantic salmon in Fortune Bay, Newfoundland with respect to release timing, life stage, post-release mortality, and post-release dispersal rates.

Aquaculture operations can result in animal aggregation over large spatial scales (Goodbrand et al 2013), and this effect extends to large predators (Uglem et al. 2014) which may serve as a source of post-escape mortality for farm fish that remain within the spatial extent of this aggregative effect (see Dempster et al. 2018). Comparing the movement of farm to wild salmon will provide data necessary to characterize relative habitat use of each group in response to aquaculture activity, and subsequently assess the relative mortality risk for these fish while in the ocean.

Farmed salmon have been selectively bred over many generations for high growth rates and must consume large amounts of food to meet the associated energetic demands (Harvey et al. 2016). These fish have spent their lives almost entirely reliant on daily feedings in cages, and fish that have escaped in to the wild are likely still attracted to feeding operations due to conditional responses developed during containment (Charles et al. 2017). Although dispersal of farm fish from their escape site is generally rapid (Dempster et al. 2018; Hamoutene et al. 2018; Skilbrei 2015), Charles et al. (2017) showed that aquatic farmed rainbow trout frequently returned to cage sites during feeding operations, and several studies from marine environments have detected 'escapees' at multiple different farm locations after release (Hamoutene et al. 2018; Skilbrei et al. 2015) suggestive of a similar trend in the marine behavior of escaped salmon. Traveling between farm sites will subsequently increase time spent vulnerable to predators due to the attractive effect farm activity also has on large marine predators. High growth rates cause farm fish to set precedence for growth rate at the cost of high mortality risk, and given that comparative growth rates do not exist in wild salmon populations, it is likely that the value of food and safety from predators differs between domesticated and wild salmonids (Biro et al. 2004).

For wild salmon in the same environments as their escaped farm-raised counterparts, it is likely that habitat use decisions are comparatively more sensitive to changes in habitat quality. Animals select habitats by valuating the ratio of mortality risk to growth rate, and this valuation is manifested in the foraging decisions of the respective animal (Werner & Gilliam 1984). In this sense, energetic demands strongly affect assessments of habitat quality, where hunger state determines the level of mortality risk an animal is willing to tolerate to obtain a meal (Alonso 2002). Lower growth rates and subsequent energetic demands of wild salmon will lower the value of food resources for these fish (with respect to the value placed on food resources by farm salmon), and more precedence is likely placed on survival when in high risk environments. Comparatively higher risk aversion in wild salmon will manifest in habitat use differences between farm and wild fish owing to differences in growth rates. Controlled release fish have shown site fidelity to farm operations despite high endemic risk levels, and it is likely that comparable data describing habitat use of wild salmon in similar environments will reflect much higher aversion to predators than farm-raised counterparts.

On Newfoundland's south coast, the direct effects of aquaculture operations on the marine behavior of wild salmon populations remain largely unexplored (but see Dempson et al. 2011) and may impact already threatened local wild salmon populations (DFO 2017). In our study, we compare the movement of wild Atlantic salmon smolts to controlled releases of farmed Atlantic salmon from Hamoutene et al. (2018). Farm fish can exhibit site fidelity to farm operations (Charles et al. 2017), and given reduced responses to predators exhibited by domesticated fish (Biro et al. 2004) and higher predator abundance around active farm locations (Chapter 3), natural predation may serve as an important means of controlling the spread of farm fish in the ocean, as recapture attempts often have low success rates (Dempster et al. 2018;

Skilbrei et al. 2015). High endemic risk levels may also affect the behavior of wild salmon, and we therefore also describe the movement of wild fish around aquaculture sites in a coastal fjord to determine behavioral responses to aquaculture-related changes in local environmental conditions. Genetic analysis has shown that farm fish are hybridizing with wild stocks along the Coast of Bays (Keyser et al. 2018), and more effective methods of limiting the possibility of farm fish entering aquatic environments must be developed and implemented, as introgression dilutes the genetic integrity of localized adaptations in wild populations (Bolstad et al. 2017; Garcia de Leaniz et al. 2007; McGinnity et al. 2003). Here, we provide data describing the movement of wild and farmed salmon around active aquaculture sites. We use these data to describe potential effect magnitude of aquaculture operations on the survivorship of both groups of fish while in the ocean, and subsequently assess how changing environmental conditions caused by marine aquaculture may affect introgression risk, and as well create potential sources of mortality for ranched salmon that escape in the ocean.

Methods

In our study, we compared movement of wild smolts from Bay d'Espoir fjord (47° 40' N; 56° 07 W) to controlled releases of farm-raised salmon in the neighboring Fortune Bay (47° 36' N; 55° 17' W) performed around the same time (see Hamoutene et al. (2018)) as data was collected on wild fish. Although not collected in the same locality, comparisons of these data streams is here used to establish behavioral responses of wild and farmed salmon to similar sets of environmental conditions present within years (i.e. how do the behaviors differ given annual environmental conditions), rather than comparisons between years which cannot account for environmental differences. As well, direct lifestage comparisons are only valid if escapees enter the ocean at the same size/lifestage and during the brief time window when wild counterparts

occupy coastal environments, a situation which is relatively unlikely to occur consistently. Farm salmon are also significantly larger than wild counterparts, thus direct life stage comparisons may be difficult to interpret given dramatic size differences. We therefore compared wild and farm salmon at different life stages monitored in the same year, to quantify behavioral differences to similar environmental conditions.

Wild salmon in our study were tracked in the Bay d'Espoir fjord located on the south coast of Newfoundland. This fjord is an important migratory pathway for Atlantic salmon smolts exiting local rivers (Dempson et al. 2011), and is also home to significant Atlantic salmon (*Salmo salar*) and rainbow trout (*Onchorynchus mykiss*) aquaculture operations present from the Conne River outflow through the entrance to Hermitage Bay (which marks the end of the fjord). Although significant portions of the fjord are licensed for aquaculture operations (> 50 potential sites at the time of our study), only 18 sites were actively producing fish at the time of our study.

We studied residency behavior of a group of salmon smolts from the Conne river (47° 54' N; 55° 41' W). The Conne river empties in to the northeast portion of Bay d'Espoir with a drainage area of 602km^2 (Dempson & Stansbury 1991). Conne river salmon populations have seen significant declines over the past decade, and marine survival is a major limitation in the recovery of these populations (DFO 2017). Smolts must travel 50km to reach Hermitage Bay (fjord exit) and the migration routes of fish originating from the Conne river have been well described (see Dempson et al. 2011) and are adjacent to active aquaculture sites throughout the Bay d'Espoir fjord.

The first 14 km of the migration pathway (the inner fjord region) contained 5 active aquaculture sites for the duration of our study. The middle fjord region is divided by Bois Island, and fish may migrate on the northern edge of the fjord through the Lampoides passage, or

through the large main channel to the south (Dempson et al. 2011). Fish traveling down the main channel may also choose to migrate through Little Passage, a small channel off the main migration corridor. Little passage is relatively narrow (200-1000m wide) and shallow (60-100m depth) (Dempson et al. 2011), and all fish traveling through it during our study were exposed to 3 active farm sites within the channel, and 3 more sites north of the channel exit into Hermitage Bay. In the outer portion of the fjord where both the Lampoides passage and the main channel meet Hermitage bay, there were an additional 3 active farm sites. (**Figure 5.1**).

Acoustic tagging and tracking (monitoring)

Forty (n=40) smolts were collected on May 16, 2016 during their annual migration window from a DFO-operated counting fence on the Conne river. All fish were removed from the counting fence and placed in a makeshift holding tank (88l plastic tote) on the side of the river prior to tagging. Fresh water was pumped directly from the river in to the tote to maintain ambient river conditions within the holding tank. Individual fish were removed from the tote and placed in an anesthesia bath (100ppm clove oil-methanol solution) (see Andersen et al. 1997) immediately prior to tagging, and fork-length (mm) and mass (g) were also recorded (**Table 5.1)**. Fish with injuries or obvious signs of stress were not used. Individually-coded acoustic transmitters (Vemco Ltd, Model V8-2x, 20.5 mm X 8 mm, 0.9 g in-water weight, 80s nominal ping delay, battery life 182 days; www.vemco.com) were surgically implanted in fish following the procedure of Dempson et al. (2011). Fish were returned to the flow through trap in the counting fence after tagging procedures, and kept for 24 h after tagging to ensure adequate recovery. After the 24 h holding period, fish were released from the counting fence back into the river (17 May).

Behavior of smolts around aquaculture sites was monitored using an array of VR2W acoustic receivers (Vemco Ltd.) placed at farm sites throughout the Bay d'Espoir fjord. Five farm sites in the inner fjord and nine sites in the outer fjord region were monitored for a total of fourteen (n=14) sites. Since there were no farm sites in operation in the middle fjord region (Lampoides passage and main channel), no receivers were placed in that location. Positioning of farm sites within bays allowed the majority of sites to be monitored by single receivers. Multiple receivers were used at four sites because the positioning and size of net-pen arrays exceeded the maximum detection ranges (c. 500m), and a total of 18 receivers were used in our array. Receivers were attached to 10m of braided nylon line using cable ties. SCUBA divers then attached one end of this line to the marker buoy mooring line on the outer perimeter of the cage site roughly 20 m below the surface. The other end of the receiver line was fitted with a small trawl float that suspended the receiver in the water column roughly 15 meters below the surface. Our array was installed prior to smolt tagging, and was monitored through the summer until retrieval in early October.

Residency behavior was measured by determining the time duration between first and last detections at farm sites. Independent residency 'events' constituted periods of residency around farm sites separated by fish movement between monitored sites, or time intervals greater than 24 hours between detections. In instances where only one detection occurred at a given site/receiver, this detection was considered a false reading and not considered in our analysis. We also calculated the time it took fish to reach the outer fjord area by determining time elapsed between release and first detection at any outer fjord site. Residency times around farm sites were compared between groups of fish using a t-test.

We also compared our data to results from Hamoutene et al. (2018) who tagged 450 farm salmon in Fortune Bay across different seasons and life stages to provide comparable data from to that of the salmon that may be used to build our understanding of behavioral differences between farm and wild fish on Newfoundland's south coast. Although comparisons between the two data sets are limited due to sample size, locality, and receiver coverage, our goal was to analyze movement and habitat use within the context of recent behavioral literature, and determine population-level responses to changing environmental conditions to improve our understanding of aquaculture-related environmental impacts. In our study, we compare data from our wild smolts tagged and released in May 2016 to controlled-releases of farm-raised Atlantic salmon from Fortune Bay performed by Hamoutene et al. (2018). We compared the behavior of wild smolts to ninety (n=90) adult farm-raised salmon released May 2015 in Fortune Bay, and as well to ninety (n=90) immature farm-raised salmon released between 2014 (n=51) and 2015 (n=39). For a full description of tagging procedures, see Hamoutene et al. (2018) and methods therein. In this study, forty-five (n=45) fish were released from two separate farm locations in Fortune Bay in Spring and Summer for a total of ninety (n=90) fish released in each season (fish were released at one site in both spring and summer, and the second release site differed between seasons (see figure **5.6**)). In all instances, fish were released in the immediate vicinity of farms, as this was assumed to reflect the most accurate simulation of an actual escape event.

We calculated movement vectors to describe the behavior of farm and wild salmon in coastal fjords. Movement vectors are the sum of individual movement steps (movement between concurrent receiver detections) and were calculated from the point of release for each fish. One vector was calculated per fish and vector subcomponents are km traveled per day and directional orientation (cardinal bearing). We also calculated the deviation of individual movement steps

from straight-line migration trajectory by examining the cardinal orientation of individual movement steps from point of release to the fjord entry into the open ocean. Movements of wild salmon are seasonally directed with fish moving to the open ocean in spring and back to freshwater in late summer/fall, and calculating deviation from seaward migration trajectory would allow us to determine how directed the movement of salmon was. We then tested for differences in vector subcomponents (velocity and movement trajectory) between wild and farm salmon using ANOVA.

Results

Wild smolts from the Conne River weighed 0.055 ± .013 kg (mean ± SD). Seventy percent (28/40) of tagged fish were detected in the marine environment, and 68% (19/28) of these fish were eventually detected around receivers in outer fjord areas. With respect to the 12 individuals never detected in the marine environment, we are unable to determine the source or mortality as high water levels washed away an acoustic mooring at the river exit immediately prior to fish tagging. We compared the behavior of our wild fish to spring-releases of farm salmon, as well as to immature farm salmon released in summer. Farm-origin fish released in the spring (n=90) weighed 2.25 ± 0.9 kg, and immature fish released in summer (n=90) weighed 0.37 ± 0.08 kg. Comparative understanding of movement behavior will be used to inform on factors affecting the spread of farm fish, the magnitude of interactions between farm and wild fish in marine environments, and relative mortality risk created by aquaculture for both farm and wild fish around active farm operations.

Fidelity to aquaculture sites

We first tested for differences in temporal residency around farm sites between groups of farm and wild salmon. We report residency behavior as a percentage value representing the proportion of time spent around farm sites relative to total time detected within the array. We compared wild smolts (n=28) to immature farm fish (n=90), and found that farm-origin fish spent a significantly higher proportion of time around farm sites than wild fish (t_{115}=9.49, p=5.5e^{-16}) (**Figure 5.2**). On average, smolts spent 0.78 ± 0.33 days (cumulative time, mean ± se) in the immediate vicinity of farms, while immature farm fish spent 15.43 ± 4.47 days around farms. We also compared wild smolts to spring-released farm salmon (n=90), and found that spring-released farm-origin fish spent a significantly higher proportion of time around farm sites than wild fish (t_{112}=4.75, p=6.11e^{-6}) (**Figure 5.3**). The 0.78 ± 0.33 days (cumulative time) spent around farms by smolts differed from spring-released farm salmon that spent 7.00 ± 3.50 days around farms. Cumulatively, total time spent within the confines of the respective receiver arrays was 20.23 ± 3.83 days for farmed fish spring releases, 38.25 ± 8.7 days for farmed fish summer releases, and 19.56 ± 2.52 days for spring releases of wild smolts.

Fjord Behavior

Hamoutene et al. (2018) showed that farm fish released in spring dispersed significantly further from their release site than fish released in summer and autumn, and autumn releases dispersed the shortest distance from their release site. Interestingly however, despite highest dispersal distances being recorded in spring-released fish, there was no significant difference in movement rate, indicating similar activity budgets for spring- and summer-released farm fish. We also detected differences in movement rates between wild (n=28), spring-released farm-

origin (n=90), and immature [summer] released farm-origin (n = 90) (F_2 = 10.81, p = 3.43e-5) (**Figure 5.4**). There was significant variation in movement rates of farm salmon compared to wild counterparts, and our data showed significantly higher movement rates in farm salmon (mean ± se for spring and summer releases respectively: 17.62 ± 2.37 & 24.79 ± 2.58 km·d^{-1}). Comparatively, wild smolts showed very little variation in movement rates (mean ± se: 2.91 ± 0.30 km·d^{-1}), and movements were consistent and progressive toward outer fjord areas, and this is supported by our analysis of movement trajectories.

Prior to comparison with wild fish, we tested for differences in deviation from straight line migration trajectories between farm fish from different release locations. No differences in movement trajectory between groups of farm fish from different release locations were detected in spring (t_{72} = 1.49, p = 0.142) and summer (t_{44} = -1.37, p = 0.177), and these fish were grouped for subsequent comparisons with wild fish. Deviation from straight line migration trajectory differed between farm (n=89) and wild fish (n=28) in springtime (t_{36} = 11.4, p = 1.495e-13)(**Figure 5.5**), as well as between wild (n=28) and immature (n=90) salmon from farm releases during the summer (t_{34} = 10.933, p = 1.08e-12). Directed movements of farm salmon (**Figure 5.6**) occurred over a wide range of cardinal bearings, while wild salmon movements were progressively directed toward fjord exit points (**Figure 5.7**).

Discussion

In our study, we described the movement of wild Atlantic salmon smolts around aquaculture sites on the south coast of Newfoundland, and compared these data to movement of farm salmon in a similar study (see Hamoutene et al. 2018) to infer differences in habitat use between the two groups of fish. We identified significant differences in the movement of farm and wild salmon, and showed that the movement of farm fish is comparatively more erratic (with respect to

deviation from direct seaward migration) and of greater magnitude than that of wild salmon, which was directed and consistent (very little variation in km travelled per day) throughout the duration of their seaward migration. We also showed that farm fish spend more time around active farm sites and traveled at higher velocities than wild salmon.

We compared data sets from two adjacent fjords containing active salmon aquaculture sites. Results from our telemetry data must therefore be considered within respect to differences between the two study sites, particularly differences in topography and receiver coverage. Our receiver array was designed to capture differences in residency behavior around farm sites, and in Bay d'Espoir we therefore monitored active aquaculture sites to determine the relative amount of time spent in the immediate vicinity of active farms versus elsewhere in the fjord environment. While analogous receiver coverage was used in Hamoutene et al. (2018) in Fortune Bay, this study also maintained receiver coverage in areas not containing farm sites, which likely provided a more detailed picture of fish movements. However, for our analysis of residency behavior around farm sites, only receivers at farm locations were considered so as to obtain similar data to those collected in Bay d'Espoir (presence/absence). Also, differences in fjord topography may have biased our analysis of movement trajectories, as Bay d'Espoir is characterized by relatively narrow channels within the larger fjord, while Fortune Bay is comparatively less restrictive to fish movements as relates to topography (see **Figures 5.6** & **5.7**). As an artifact of both receiver coverage and fjord topography, therefore, fish in Fortune Bay are therefore able to move across a much wider range of cardinal bearings than fish in Bay d'Espoir. Despite this, had the behavior of farm fish been similar to wild counterparts, it is likely that mean trajectory deviation values for both groups of farmed releases would have been substantially lower, indicating more directed movements toward fjord exit points, rather than

those we observed occurring over a wide bearing range. This analysis, however, was performed to supplement our analysis of residency behavior and was not intended to provide primary evidence for observed behavioral trends in our groups of tagged fish.

Local salmon populations from the Conne river have seen significant declines in the past decade (DFO 2017) and mitigating the risks that aquaculture operations pose to these fish in marine environments is essential, as interactions between aquaculture operations and wild salmon populations have been under-described in the western Atlantic. Movement of escaped farm fish was compared to that of wild salmon to identify potential risks for wild fish resulting from farm activity, as discrepancies in habitat use between the two groups may be exploited to bolster the efficacy of recapture attempts (with minimal risk for wild salmon), and as well to identify potential behaviors that leave farm salmon comparatively more vulnerable to natural predation around aquaculture sites. Wild salmon may be directly affected by marine aquaculture operations during periods of residency in coastal fjords (seaward smolt migrations and when returning to rivers to spawn), and fish originating from the Conne river must navigate through significant farm activity throughout the entirety of their coastal migration (Dempson et al. 2011), creating high probability of interaction with aquaculture operations and/or escaped fish in the ocean. Controlled release experiments have shown that farm salmon are subject to high mortality in the wild (Hamoutene et al. 2018; Skilbrei et al. 2015), and relative differences in movement behavior between farm and wild salmon observed in our study may provide explanation for these differences.

High post-release mortality in farm-origin fish may be partially attributed to increases in predation risk. Despite size differences between groups of wild and farmed fish used in our study, higher movement rates of farm fish may be associated with high levels of predation risk,

as increasing activity levels increases predation risk (Anholt et al. 2000; Werner & Anholt 1993). As well, farm salmon are selected for high growth rates and consequently have significantly higher energetic demands than wild counterparts, necessitating a higher food intake rate (or consumption of higher-quality food) than wild fish (Harvey et al. 2016). Charles et al. (2017) showed that environmental cues from farm operations indicating feeding activities attracted farm fish from experimental releases to the immediate vicinity of cages, and although this study was performed in fresh water, it is likely that similar trends exist with farm fish in marine operations where Hamoutene et al. (2018) showed that more than 76% of released farm fish visited multiple farm locations in Fortune Bay and remained for periods of up to 8hr despite rapid dispersal after the initial escape (or release, in this case) event. The spatial scale of marine farm operations mandates that fish move substantial distances to utilize feeding periods at different sites, which would explain significant differences in movement rates that we observed between farm and wild fish. Comparatively less fidelity to farm activity exhibited by wild fish may supplement the idea that faster seaward progression by smolts in our study relative to previous years (2007 & 2008; see Dempson et al. 2011) was a response to increased predation risk. Although seaward progression was faster than previous years for wild smolts, their movement rates (km/day) were still substantially lower than both groups of farm fish (**Figure 5.4**), and alongside differences in metabolic demands, this may also be in part explained by size/life-stage differences (Bøe et al. 2020). As well, larger fish should be subject to less predation than smaller counterparts,

Lima and Dill (1990) proposed that predation risk, displayed in equation 1 as probability of death endemic to the respective habitat (P_{death}), is comprised of three components that together dictate the magnitude that predation risk affects animal behavior. Rate of encounter (α),

probability of death given an encounter (*d*), and time spent vulnerable to predators (*T*) affect mortality rates in prey individuals, where

$$P_{death} = 1 - \exp(-\alpha dT) \quad [5.1]$$

Assessment of each allows animals to effectively control the level of predation risk they experience through habitat use decisions, and the overall impact of each component is mediated by the respective animal's energetic demands (Alonso 2002). Data from our study suggests that the outcome of equation 5.1 differs between farm and wild salmon based on observed differences in movement behavior and habitat use. One factor contributing to this differential outcome is likely differences in behavioral phenotypes of farm and wild salmon, and can be better understood by breaking down *d* into its three subcomponents, where after being encountered, the probability of death depends on probability of attack, probability of capture given an attack, and probability of death if captured (Lima & Dill 1990). In this sense, *d* can be expressed as:

$$d = P_{attack} * P_{capture} * P_{death} \quad [5.2]$$

Domesticated salmonids have a higher willingness to tolerate risk exposure (Johnsson & Abrahams 1991; Biro et al. 2004), and should show preference for high quality food resources (excess feed) found at farm locations despite predator preference for these areas. Increased time spent in the vicinity of aquaculture will increase encounter rates with predators (higher values of α), which the impact magnitude of *d* on equation 5.1 in the sense that *d* will always equal zero unless $\alpha > 0$. Wild populations are highly adapted to local environmental conditions (Garcia de

Leaniz et al. 2007), whereas farm populations are selected for high growth rates, and Biro et al. (2004) showed that domestic trout strains took more foraging risks and grew faster than wild strains, but mortality rate was strongly affected by the risk environment. High mortality rates accompanied increases in predation risk, and in sea cage environments where endemic risk levels are increased by predator attraction (Uglem et al. 2014), it is likely that populations with high growth rate phenotypes experience similarly high mortality rate due to selection for these phenotypes.

An animal's activity level also affects both growth rate and mortality risk, where more active individuals encounter food items at higher rates, but also are subject to higher encounter rates with predators (Anholt et al. 1993). For farm salmon with higher activity rates than wild counterparts, time spent vulnerable to predators (T: equation 5.1) is significantly higher than for wild fish in sea cage environments where predators are aggregated. Increasing values of T increases P_{death} in a given habitat (as long as $\alpha > 0$ and $d > 0$), and populations of farm salmon co-occurring with wild counterparts should therefore have higher mortality rate due to the combination of increased time duration spent vulnerable to predators, increased likelihood of encounter, and subsequent increased likelihood of attack. High post release mortality has been documented in many controlled release experiments (Hamoutene et al. 2018; Skilbrei et al. 2015), and our results have subsequently provided mechanistic understanding of factors contributing to this mortality for farm fish in marine environments.

Dempson et al. (2011) reported the residency time of Conne river smolts from 2007 and 2008 in the coastal fjord during seaward migration, and found mean (± S.E) residency times of 37 ± 1.4 and 45 ± 2.3 days respectively. Mean residency time (± S.E) within the coastal fjord for smolts tagged in our study was 25 ± 2.58 days, showing significantly more rapid progression to

fjord exit points than smolts in 2007 and 2008. Decreased temporal duration within the fjord may be partially driven by changing environmental conditions resulting from aquaculture activities, where increased predator abundance creates perceived differences in habitat quality for wild salmon. Although we previously stated that high activity budgets in farm fish likely leads to high post-escape mortality, the relative impact that activity level has on mortality rate is contingent on the animal's perception of environmental quality. For farm fish with comparatively reduced responses to predation risk, we concluded that high activity budgets accompanying high growth-rate phenotypes lead to high mortality rates because of comparatively reduced responses to predators. For wild fish whose behavior is likely more sensitive to *both* predation risk and foraging demands, decreasing time spent within the fjord will ultimately reduce α and *d* with respect to equation 5.1 by reducing the overall time spent vulnerable to predators (*T*: equation 5.1) in high risk areas around farm sites. Although coastal fjords are often the first feeding opportunity for salmon smolts after entering the ocean, residency time of wild fish within these habitats reflects the relative value of these feeding opportunities with respect to mortality risk, and differences in fjord residency time between smolts from our study and those from Dempson et al. (2011) suggest that mortality risk around farm operations outweighs potential foraging opportunities for wild fish. In this sense, activity level likely has different effects on mortality rates in farm and wild salmon due to differences in risk valuation between the two groups of fish.

We have argued that differences in movement and habitat use between groups of farm and wild salmon will cause differences in mortality rates between the two populations. Although there were factors that may potentially be interpreted as confounding, such as size and life-stage differences, it is important to document comparative differences between the movement of farm and wild salmon in these instances, as it is highly unlikely that the size and life-stage of escaped

fish corresponds exactly to that of wild fish at the moment of escape. As such, cohorts of wild smolts migrating through coastal environments may coincide with escaped salmon of variable life stages that are prone to the same set of environmental conditions as wild smolts. Quantifying behavioral differences between these groups as we did in our study is therefore important, as we showed how a general behavioral principle (movement rate) can be used to infer how the same set of environmental conditions will have differential effects on farm and wild salmon.

Our results must be also considered with respect to the rate of escape from farm sites. In rare instances, major escape events can occur where large numbers of fish escape in to the ocean in a single event. More than 20,000 fish escaped containment in 2013 from a farm site in Hermitage Bay, located on Newfoundland's south coast, and in instances such as this it is likely that natural predation may not be as affective in limiting the proliferation of escapees in the ocean. Major escape events will significantly reduce P_{attack} for individuals due to numeric risk dilution (see Foster & Treherne 1981), where the probability of attack on a given individual depends on the number of prey items accessible to predators. With respect to equation 5.1, the magnitude of the escape event (# individuals) will not change values of α and T as we see no reason to assume that post escape movement behavior will change with escape magnitude. However, major escape events effectively swamp marine environments with potential prey for large predators, and if escape magnitude exceeds predation rate on farm fish, the likelihood of these fish surviving to reach spawning locations in fresh water increases significantly. Data we have provided suggest that marine environments can likely tolerate slow leakage of escapees from farm sites with little introgression risk due to the expression of behavioral phenotypes subject to high predation rates. Determining relative introgression risk as a function of escape

magnitude therefore represents a crucial next step in developing our understanding of aquaculture-related risks for wild salmon populations.

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Figures & Tables

Table 5.1. Tagging information from wild smolts tagged in the Conne River in May 2016.

V8 ID	**Length (cm)**	**Weight (g)**
43268-1242129	19.8	58.9
43269-1242130	20	50
43270-1242131	21	72.5
43271-1242132	20	59.5
43272-1242133	18.5	51.5
43273-1242134	19	69
43274-1242135	18.5	41.6
43275-1242136	17.5	46.9
43276-1242137	19	51
43277-1242138	17.5	43.1
43278-1242139	19.6	59
43279-1242140	18.8	49
43280-1242141	18.7	54
43281-1242142	19.5	57.2
43282-1242143	27.5	124
43283-1242144	19.5	60.1
43284-1242145	19.4	57.2
43285-1242146	18.3	57.9
43286-1242147	20.5	62.8
43287-1242148	18.3	47.5
43288-1242149	18	47.5
43289-1242150	17.8	45
43290-1242151	18.5	51
43291-1242152	17.5	46.3
43292-1242153	19	50
43293-1242154	18	49.5
43294-1242155	19	59
43295-1242156	19	59.1
43296-1242157	21	63
43297-1242158	18	49.5
43298-1242159	17	50
43299-1242160	18	47
43300-1242161	18.5	54.8
43301-1242162	19.5	58
43302-1242163	17.8	48.5

43303-1242164	17.5	46
43304-1242165	18	45
43305-1242166	18.5	47.1
43306-1242167	18.5	56
43307-1242168	18.5	50.5

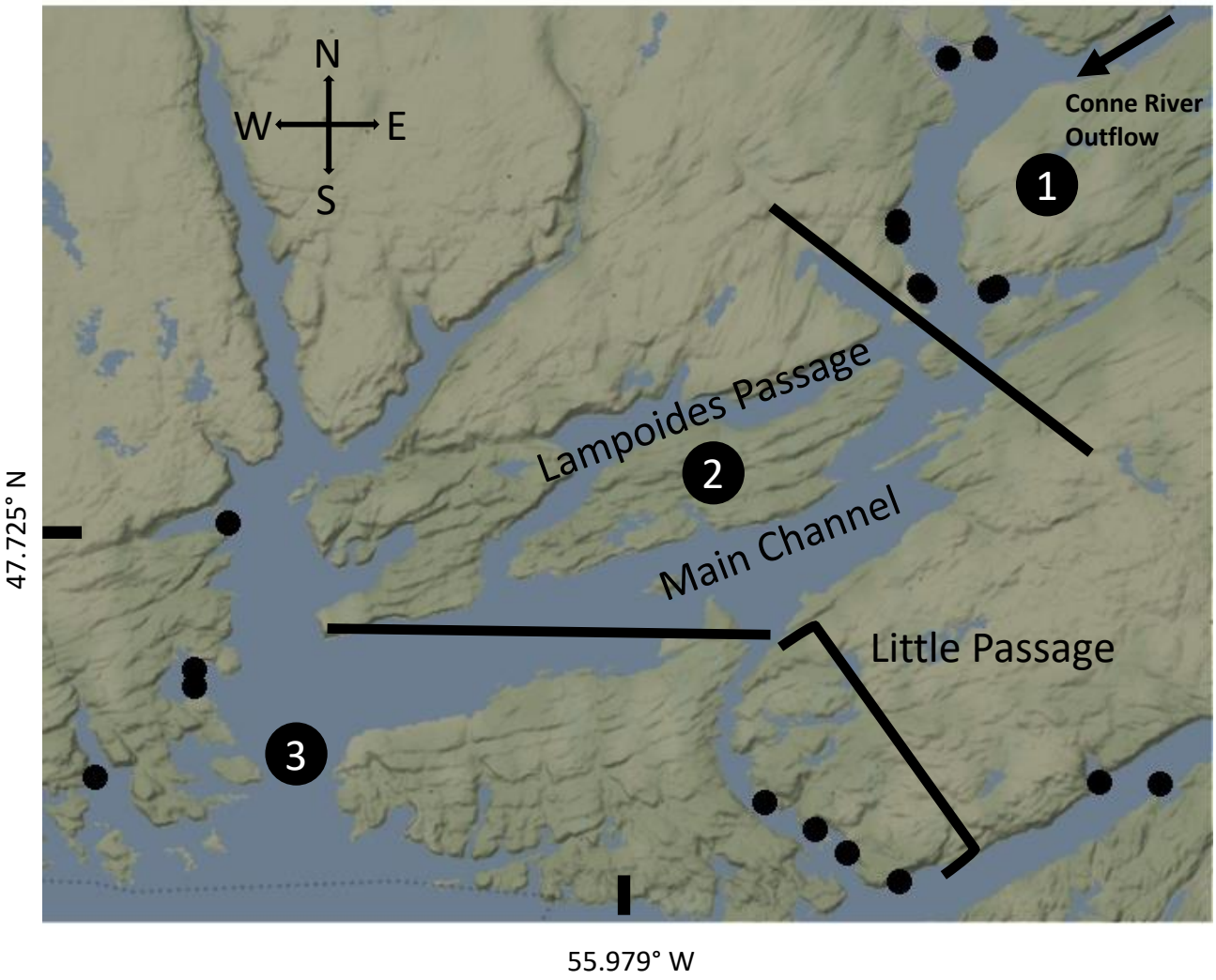

Figure 5.1 Map of Bay d'Espoir showing location of all monitored aquaculture sites (black dots). All sites were monitored from May-October of 2016 and detections occurred on all receivers except for one location (southwestern-most receiver). Black circles with inlaid numbers 1-3 indicate inner, middle, and outer fjord zones, respectively. Three southern-most sites in area 1 required the use of two receivers to cover the entirety of the site, and likewise one site in area three required two receivers (two overlapping points indicates the use of two receivers at the respective site).

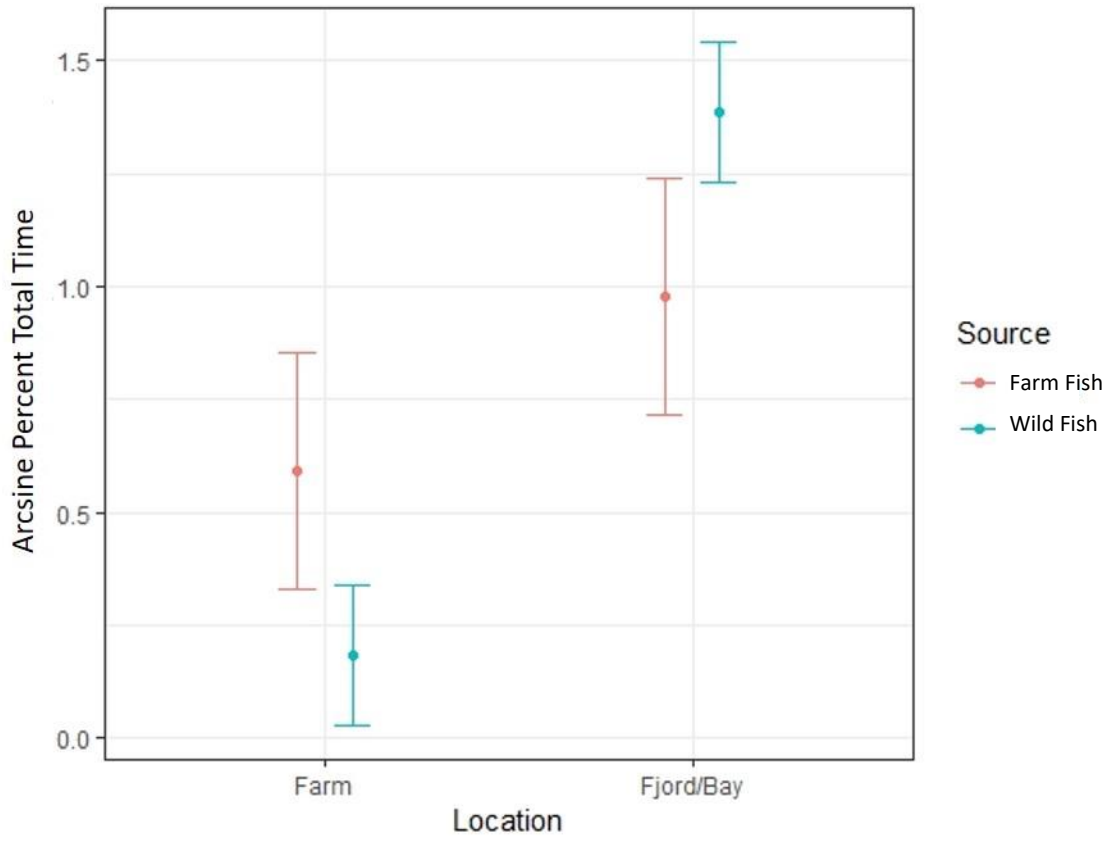

Figure 5.2 Data shows percent total time spent by groups of wild smolts (n=28) and immature farm-origin salmon released in summer (n=90) at farms versus in the larger bay environment. Error bars are ± one standard error from the mean.

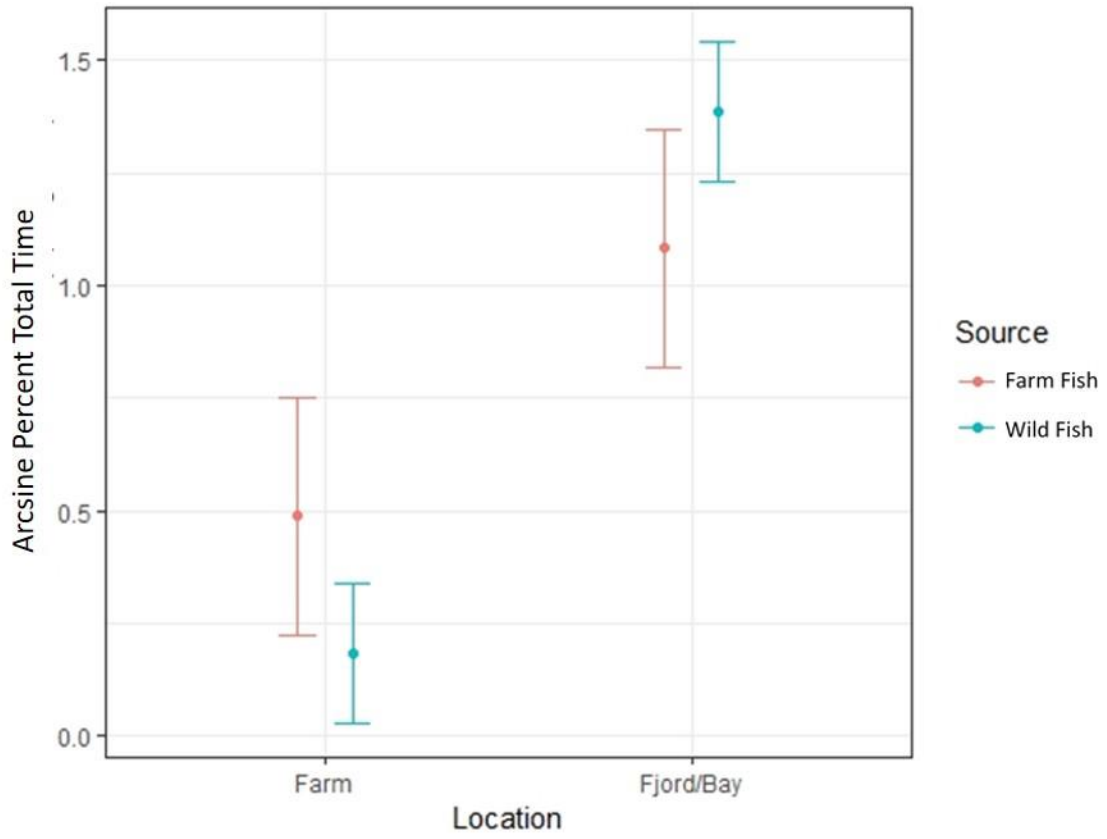

Figure 5.3 Data shows percent total time spent by groups of wild smolts (n=28) and spring-released farm-origin salmon (n=90) at farms versus in the larger bay environment. Error bars are ± one standard error from the mean.

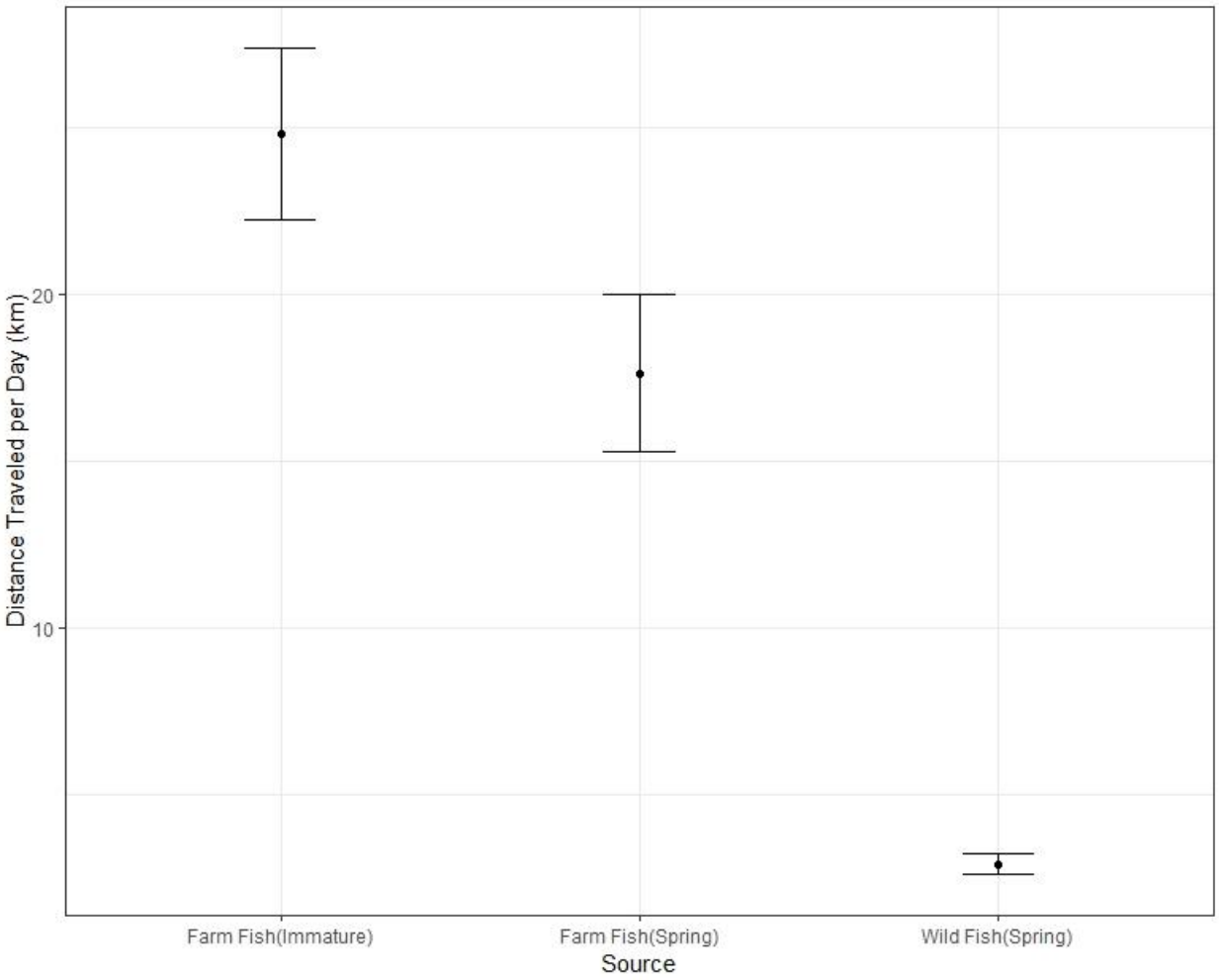

Figure 5.4 Mean distance traveled per day (km per day) for groups of wild salmon smolts (n=28), spring-released farm salmon (n=90), and immature (summer-released) farm salmon. Error bars are ± one standard error from the mean. Post-hoc Tukey-test showed that wild fish differed significantly from both spring ($p = 0.006$) and summer ($p < 0.0001$) farm-released fish, and groups of farm fish did not differ significantly from one another ($p = 0.07$).

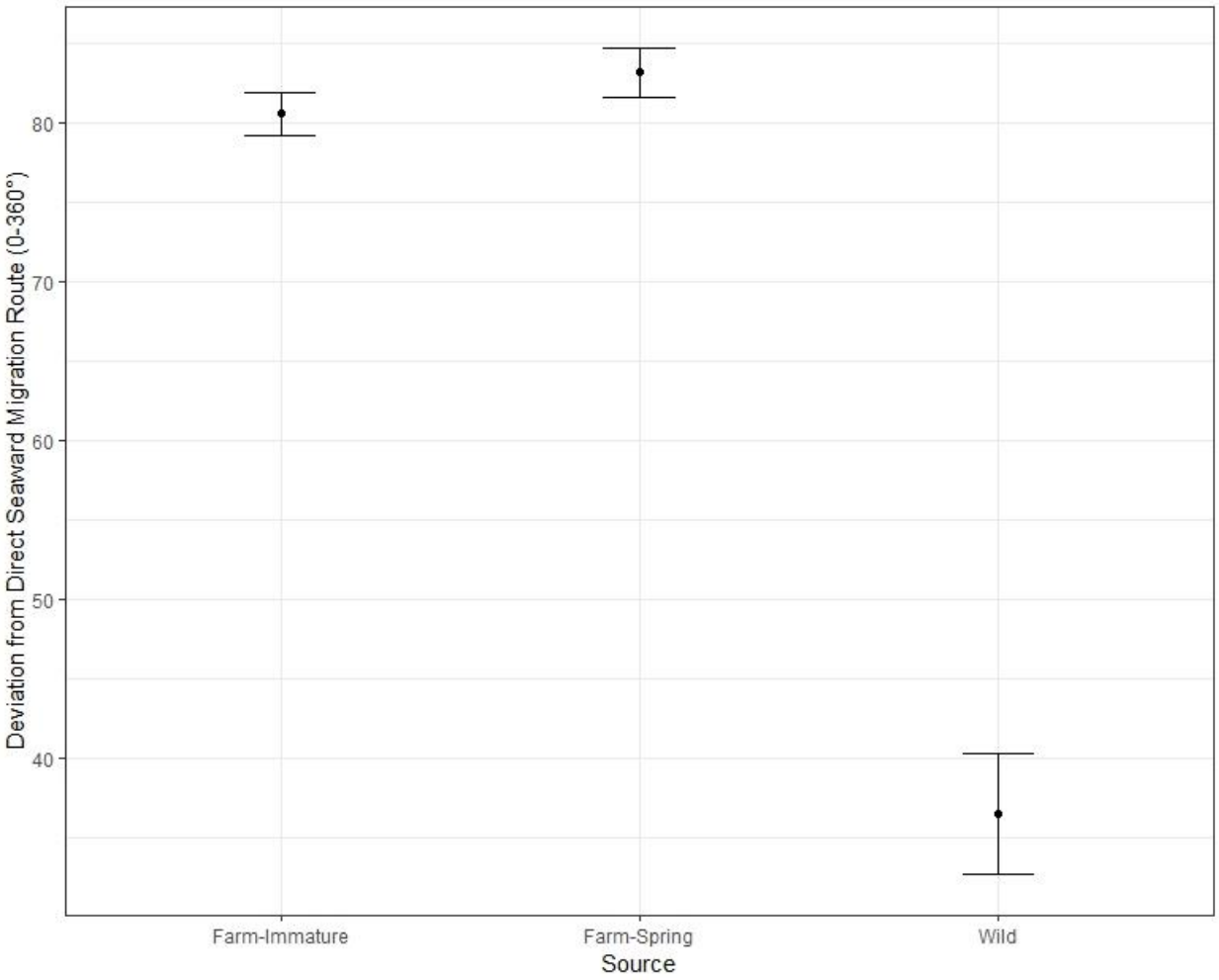

Figure 5.5 Mean deviation (°True) from direct seaward migration route for farm and wild salmon. Error bars are ± one standard error from the mean.

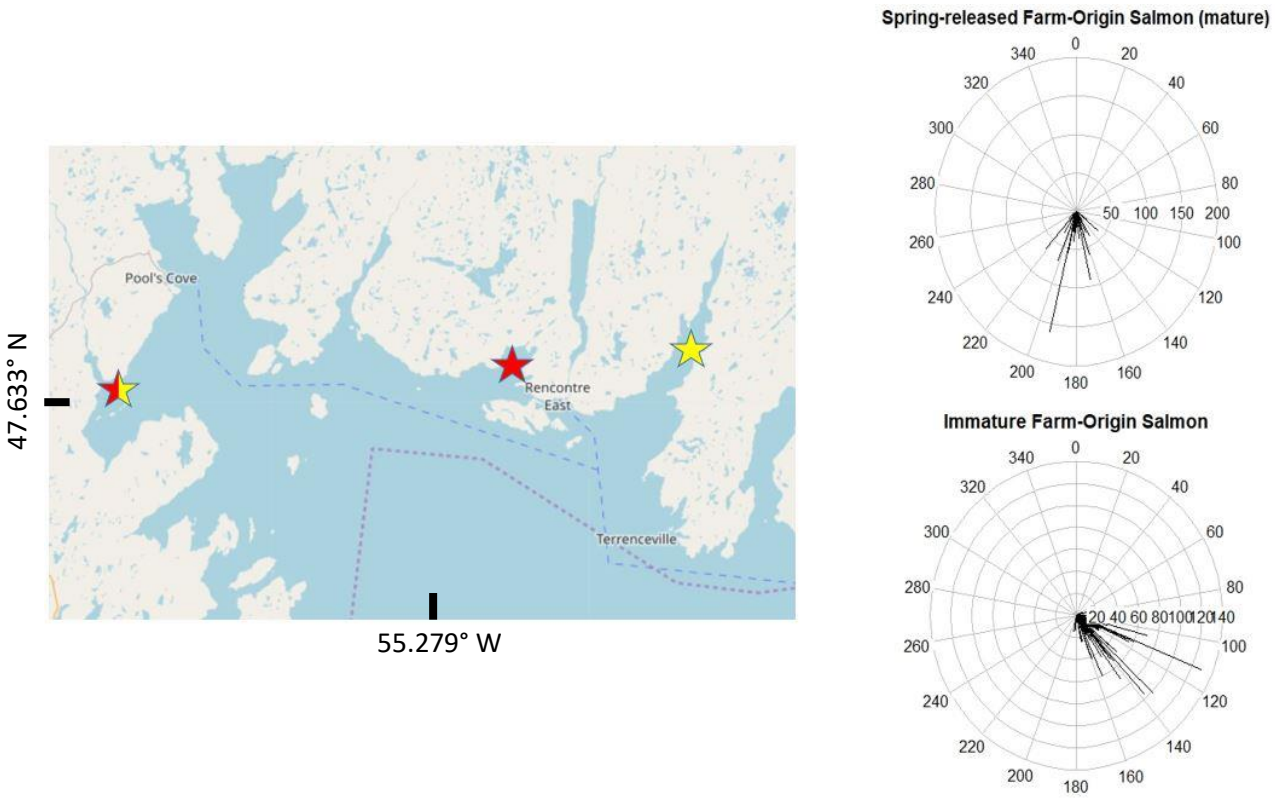

Figure 5.6 Movement vectors of farm-origin salmon from release points. Line length indicates average distance traveled per day (km), and cardinal orientation indicates mean directional heading of the respective fish. Stars indicate release locations. Red stars indicate releases of immature fish and yellow stars indicate spring-released salmon. Stars with both red and yellow indicate that releases from both groups occurred at the indicated location.

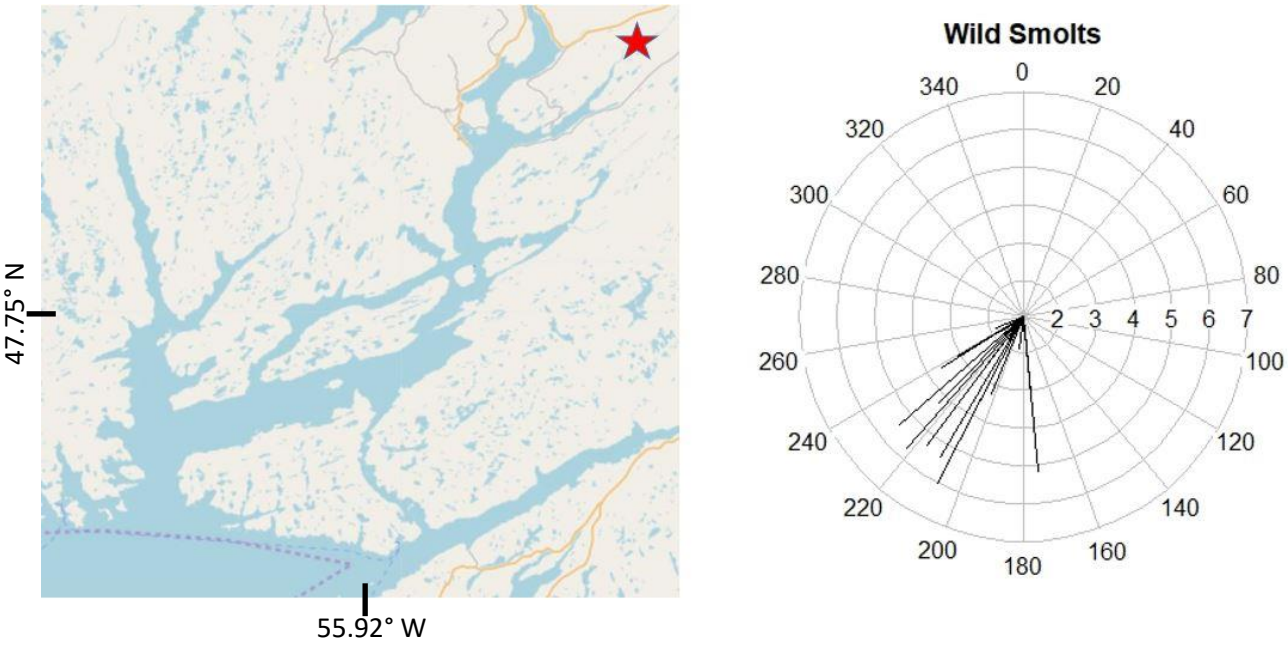

Figure 5.7 Movement vectors of wild salmon smolts. Line length indicates average distance traveled per day (km), and cardinal orientation indicates mean directional heading of the respective fish. Red star denotes release location of fish after tagging procedures.

Chapter 6. General Conclusion

In this thesis, I examined the effects of marine sea cage aquaculture on the structure and function of pelagic ecosystems. First, I developed a method to quantify predation risk observations by identifying patterns in fish school morphologies that result from spatial variation in risk levels, as we are currently lacking an effective method to quantify predation risk independent of concurrent observations of predators. Second, I examined the effects of aquaculture activities on top-down and bottom-up ecosystem drivers to assess aquaculture-related changes to the dynamics of pelagic marine ecosystems. Third, I described marine movement patterns between groups of farm and wild Atlantic salmon around sea farm sites to increase our understanding of behaviors and environmental factors that affect marine survival rates between the two groups in areas of high farming intensity.

In Chapter 2, I used hydroacoustic observations of fish schools as a barometer for predation risk levels without making direct observations of predators. I showed that schools of fish in areas with high predator abundance are significantly more vertically stratified than counterparts in areas with low predator abundance, suggesting that schools in high risk areas (areas with higher predator abundance) sacrifice hydrodynamic benefits of schooling in favor of better predator detection capabilities (see Abrahams & Colgan 1989; Hemelrijk et al. 2015). Although the importance of top-down control in pelagic ecosystems is well recognized (e.g. Verity & Smetacek 1996), our understanding of predation risk and its effects on the dynamics of fish schools (e.g. Nøttestad et al. 1996; Axelsen et al. 2001; Nøttestad et al. 2002) and individual animals (e.g. Heithaus and Dill 2006; Wirsing et al. 2007) has been developed from studies utilizing direct observations of predators to substantiate suggestions that the behavior of interest is the result of (or at least partially driven by) predation risk. In my approach, I inverted this

methodology where instead of using predator observations to describe the risk environment, I instead quantified strength of antipredator behavior displayed by fish schools based on known responses of schools to predators/predation risk, and used these data as a means to describe the risk environment in pelagic ecosystems.

In Chapter 3, I utilized the method developed in chapter 2 to determine the relative effects of aquaculture activities on top-down ecosystem control. I observed no difference in both the detection rate and size of fish schools between active and fallow aquaculture sites, suggesting relatively homogenous distribution of schooling fish across the larger environment regardless of site activity status (active of fallow). I did observe differences in school morphologies between active and fallow sites where schools detected in bays containing active farm sites were nearly six-times more vertically stratified than schools detected in fallow bays. I also recorded the proximity of predator sightings to aquaculture sites, and of the 12 total predator sightings (two occurred during a different portion of our study in an adjacent fjord containing significant farm intensity) all occurred in immediate proximity (<1km) to either an active farm, or a bay containing active farms. The same system was surveyed by Goodbrand et al. (2013) who found that active farm sites contained significantly more fish biomass than licensed but unused sites. Since this time, aquaculture infrastructure has been installed and fish produced in all bays surveyed by Goodbrand et al. (2013), and I was therefore able to compare active and fallow bays, all with recent history of active farming (within 3 years), to quantify ecosystem-level responses to farming operations. Compared to results from Goodbrand et al. (2013), relatively homogeneous distribution of fish between active and fallow sites observed in my study suggest that the effects of aquaculture activities span beyond periods of farm activity. As well, I was only able to observe snapshots of these systems from our hydroacoustic data, and it is next important

to add data with appropriate temporal dimensions to describe behavioral interactions between predators and prey in this system. Significant proportions of ecosystem-level activity can be compressed into very short temporal windows in undisturbed pelagic systems, and it is important to determine if environments containing aquaculture operations function similarly, or if addition of artificial resources for pelagic animals (food and structure) changes the dynamic behavioral cycles of animals in undisturbed systems (see Benoit-Bird & McManus 2014).

In chapter 4, I examined the effects of aquaculture activities on bottom-up ecosystem processes. I quantified regional trends in primary productivity between the three major oceanographic bays on the south coast of Newfoundland, and compared these trends to hydroacoustic data quantifying the distribution of fish and zooplankton between active and fallow farm sites from Harbour Breton through Fortune Bay. I observed significant increases in primary productivity across years within each of the three major bays, with the highest productivity levels observed in Placentia Bay relative to Fortune Bay and Bay d'Espoir. As well, despite observations of a distinct effect gradient in the distribution and abundance of zooplankton around farms in temperate regions (Fernandez-Gonzalez et al. 2013), I observed no such differences in the distribution of zooplankton between active and fallow farm sites, which may be a consequence of higher endemic productivity cold water environments. Differences between regional productivity and zooplankton distribution/abundance merit further investigation as it is unclear if regional productivity trends are a consequence of aquaculture activities or larger ecosystem processes.

In Chapter 5, I compared the movement of groups of farm-raised and wild Atlantic salmon in areas with high farm intensity. My results indicate that farm salmon maintain higher movement rates than farm fish, which likely leads to comparably higher mortality for farm fish

in the ocean (after escape) than wild counterparts. Movement behavior within coastal fjords also differed significantly between the two groups with respect to migration trajectories. Wild fish showed significantly less deviation from straight line migration trajectories than farm fish, where movement vectors indicated steady progression toward fjord/bay seaward exit points, while farm salmon movements were less directed towards seaward exit points and likely affected more so by farm activity. Analysis of residency time around farm sites showed that both groups of controlled release farm fish (immature fish in summer, mature fish in spring) spent significantly more time around farm sites than wild smolts, which would suggest that movements of farm fish are likely the result of attraction to farm sites (similar results published in Charles et al. 2017). As well, although movement rates ($km \cdot d^{-1}$) of wild fish were significantly lower than both groups of farm fish within coastal fjords containing farm operations, they did progress significantly faster through the Bay d'Espoir fjord than in previous years (see Dempson et al. 2011) which would suggest an adaptive response to aquaculture activities that likely results from changes to the risk environment. Predator attraction to active farms, coupled with reduced antipredator behavior (Biro et al. 2004) and high movement rates observed in our study, likely lead to comparably higher mortality rates for farm fish relative to wild counterparts around farm sites.

Cumulatively, my results show that the mechanisms responsible for the ecosystem-level effect generated by sea farms are partially driven by altered predator behavior and resource predictability. I was able to survey bays containing aquaculture net pens during active and fallow periods, which allowed me to determine the effects of productivity cycles (sites transitioning from productivity periods to ones of inactivity or vice versa) on processes and factors that bear significant influence on pelagic ecosystem structure. Goodbrand et al. (2013) documented a larger spatial effect scale associated with sea-cage aquaculture than previously

documented with recognition that farm operations create an 'ecosystem-level effect' on marine environments (Dempster et al. 2009), and my results corroborate these findings in that I was able to identify behavioral patterns of fish schools that were indicative of larger ecosystem processes (predation risk and resource availability). However, persistent aggregations in bays recently utilized but currently not in active production periods suggest that we do not yet have a clear understanding of mechanisms that underlie the longer-term footprint of aquaculture activities, especially considering how the Fortune Bay system has changed relative to surveys performed by Goodbrand et al. (2013). In my study, I employed a novel application of hydroacoustic data to identify patterns in fish school morphologies present across the larger spatial environment that suggest adaptation to increased risk levels associated with farm activity. The persistence of aggregations around active farms suggests that enough food resources are available to balance the effects of increased predator abundance. As well, wild salmon spent significantly less time in the coastal environment where farms are present than in previous years, which may also be the result of a changing risk environment as wild salmon smolts are most vulnerable during early phases of their marine migrations.

Overall, this thesis has provided information necessary to inform on the sustainable development of the aquaculture industry in Newfoundland, with respect to potential aquaculture-related effects on local, wild salmon populations. Significant farm activity currently exists in two of the three major oceanographic bays along Newfoundland's south coast, and expansion in to the third is ongoing. Much concern has been raised regarding potential negative effects of these activities on wild salmon stocks whose natal rivers coincide spatially with significant farm activity, and my results suggest that wild ecosystems are adapting to changing environmental conditions. Our schools data indicates that pelagic fishes are adapting to landscape-level changes

to the risk environment, and decreased time spent within coastal environments for my wild smolts relative to results from Dempson et al. (2011) suggests that wild salmon may be doing the same. Sighting of large predators exclusively around active farm sites concurrently indicates that changes to the risk environment are most pronounced in response to farm activity, and that distribution of active and fallow farm sites after the initial onset of farming activities creates spatial gradients in predation risk. Future industry expansion may therefore have reduced effects on wild salmon populations if bays containing salmon rivers are left vacant. As well, wild salmon showed little in the way of residency behavior around farm sites during coastal migrations despite availability of excess feed and physical structure, and identifying critical coastal migration routes for local salmon populations may help to identify areas where the effect magnitude of aquaculture operations on wild salmon populations is currently greatest (i.e. farms occur along migration routes), and reducing or moving operations out of these areas may therefore help to mitigate potential future impacts of farm activities on wild salmon.

Beyond the scope of aquaculture operations, human activities are prevalent in many other areas of the world's oceans. At their foundation, results from of my thesis chapters are driven by the aggregative effect generated by sea cage aquaculture, an effect that also occurs as a byproduct of other human activities in pelagic marine environments like offshore oil platforms, for example. We showed that aquaculture operations can change pelagic ecosystem structure by maintaining multi-trophic aggregations of wild animals at large spatial scales, and that the mechanisms driving this change concurrently drive behavioral patterns of animals that contribute to overall ecosystem structure. With respect to other systems affected by human activities, my results illustrate the importance of understanding primary mechanisms through which the respective activity affects the ecosystem it occupies. Offshore oil platforms, for example, likely

do not provide the same level of direct, [artificial] predictable food resources for wild animals that are provided by daily aquaculture feedings, and the effect of these platforms on wild animals may therefore be comparatively less-driven by artificial food resources, but similarly so by artificial physical structures. Therefore, while similar principles may be applied between to the study of offshore oil platforms and aquaculture cages with respect to the effects of artificial physical structures, differences in underlying mechanisms (artificial food enrichment via daily cage feedings at sea farms versus offshore oil platforms around which daily food enrichment does not occur at nearly the same level) may have differential effects on the behavior and utilization of these sites by wild animals. With increasing development of marine environment for human endeavors, it is imperative that we identify the primary mechanisms through which these artificial additions to marine environments institute ecosystem change, and apply this knowledge towards understanding the implications of this ecosystem change for species endemic to the affected area. Regardless of the nature of human ingression, however, the simple fact remains that the addition of artificial resources, whether they be food, structure, refuges, or otherwise, create novel ecosystems and environments for wild animals to utilize. My results indicate that the unique set of underlying mechanisms (excess feed and physical structure) dictate the behavior of animals attracted to these sites within the new set of ecological parameters created by the presence of sea farms, and in order to understand the behavior of animals in other instances where human activities have affect marine ecosystems, researchers must first identify the primary mechanisms through which the activity generates an ecosystem-level effect.

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